



Communication and Sexual Selection in the Barking Gecko (Ptenopus kochi)

Daniel Adam Polakow

*Submitted for fulfilment of the degree
Master of Science
(M.Sc)*



***Department of Zoology
University of Cape Town***

The University of Cape Town has been given
this title in whole or in part. Copyright is held by the author.



The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

**To
Joshua
Julian, Inessa
Triton, Peter, Apollo
Russell, Lisa, Danielle, Pan and Nicolas
- the most beautiful people
in my world.**

' Won't you help to sing, these songs of freedom ...'

**Bob Marley
Redemption Song (1980)**

Abstract

This study focused on elucidating the functional significance of some aspects of the behaviour of Koch's barking gecko, *Ptenopus kochi*, during a field season conducted at the Desert Ecology Research Unit in Namibia for four months in 1995. *Ptenopus kochi* is a terrestrial species, and males were observed calling from their burrow entrances in the dry Kuiseb river bed during the hot summer months. First, aspects of competition among calling males were investigated. Calling males were seen to be non-randomly distributed relative to one another with evidence for regularity of spacing in dense aggregations. Sound intensity was investigated as the mechanism of spacing, and was mathematically modelled to gauge how the intensities of the calls of nearest-neighbour males overlapped. Results revealed a constancy at which neighbouring call intensities overlap, and playback experiments ratified the presence of a critical intensity threshold in the population, beyond which male tolerance broke down. These results suggested that spacing in *P. kochi* is vocally-mediated and that sound intensity acts as the proximate cue through which individuals gauge the closeness of neighbouring males. Second, the inter-relationships between call features of *P. kochi*'s vocalisation, and how these features related to both intrinsic (morphological) and extrinsic (ambient) sources of variability were analytically explored. The principles of information theory and individual recognition by voice were used to gauge the variation manifest in the features of *P. kochi*'s call. A novel statistical method for disentangling the influence of incidental sources of variation from 'signal' features in animal voices was developed. Results showed how once the predictable covariance in call structure was removed, the calls of *P. kochi* males were rendered statistically indistinguishable from one another. Several descriptor measures of *P. kochi*'s vocalisation were seen to be highly dependent on meteorological determinants, as was nightly chorus duration. Lastly, mate-choice in *P. kochi* was explored using correlational evidence. Results revealed that mating success was closely linked to individual male differences in display effort and chorus site burrow activity, and less to morphological or territorial characteristics. Counter-intuitively, a positive relationship between call rate and chorus site residency was found in males, suggesting a possible role for classical condition-dependence in the evolution of female mate preference. Aspects of mate choice, together with the emergent importance of residency in this study were discussed and some ideas suggested for further research.

Declaration

I declare that this thesis is my own work. It is being submitted for the degree of Master of Science at the University of Cape Town, South Africa. It has not been submitted before for any degree or examination at any other university.

Signed by candidate

Signature Removed

Daniel Adam Polakow

Acknowledgements

Mom and Dad for your continued succour. My capricious pursuits would not be possible without your unfailing support and love. Thank you.

My supervisors: Jenny Jarvis for your cardinal support and much appreciated encouragement over the last two years. Michael Cherry, too, for your support and for your helpful advice. Steven Telford, for not only being an impressive supervisor, but also for being a very special friend. Thanks Steve.

The Foundation for Research and Development and the University of Cape Town for much appreciated financial support.

Mary Seely and the Desert Research Foundation of Namibia for being there with all the logistical sustenance and the Ministry of Environment and Tourism, Namibia for their assistance.

To the Gobabeb endemics - Karla du Preez, Derick du Toit, Hilde Gevers, Lilo Nghinanwame, Susanne Peters, Teresa Sguazzin and Juliane Zeidler. Thanks for the company girls.

Vihlo 'Snake' Mtuleni - for the most beautifully humbling perspective on the world. Thanks Snake, and good luck.

Frank Echardt for the tremendous artery-clogging fry-ups every morning, afternoon and evening for several months in the desert. Thanks also for waking me at 2.30 a.m on those freezing mornings - when your enthusiasm got the better of your good judgement - to watch the fog roll in and to witness the snow.

Rüdiger and RÜth Rössl for the most superb introductions to the joy of German cooking, handrearing and loving fluffy toys, and the art of uncontrollable sweetness and cheerfulness. Thanks RÜdy for translating bits of the German literature for me.

Lastly, to the BBC camera team for the laughs. So sorry we had to witness your eating of the 'gravel-plains Rössl' jam and liquorice cake. I hope that both your stomachs and senses of humour recover.

Dave Tilch for the acoustical engineering, for the anechoic chamber design, the sound blaster advice, for the linear algebra checks and for the not so linear Tsitsikamma adventure. Ian Davidson for 'timeous' electronic skills, Shimrit Lahav-Ginott, Gary Davies and Lorraine Egan for valuable field assistance. Rupert Marshall for the Bayesian foresight. Special thanks to Wolf Haacke for kindly providing a comprehensive set of reprints on the *Ptenopus* work, and for the useful discussion.

Patricia Backwell, Michael Beecher, Rob Brooks, Neil Caithness, Mike Cherry, Mark Cooper, Derick du Toit, Jenny Jarvis, Mike Jennions, Bill Hamilton, Kate Lessells, Justin O'Riain, Paul Sherman, Andrew Spinks, and Steve Telford for some very valuable discussion and input.

Bill Hamilton, Andrew Scherrer, Yehudah Werner and Gerry Wilkinson for the encouragement. Douglas Hawkins - thanks for listening so patiently from so far and so high to my multidimensional covariate-adjusted ideas, and for so perspicaciously transforming them into a statistically acceptable distribution.

Graham Alexander, Michael Beecher, Sharon Doherty, Neville Eden, Mr. Jongens, Mervin Mason - for being there. Penny Beamish and Janine Dunlop for the reference hunting.

Hazel Corrin, Colette Franz, Onno Huyser, Quinton Johnsone, Harry Kentrotus, Rael Loon, Lance Myers, Throshni Naidoo, Lorenzo Prendini, Andrew Pringle, Michele Sanders, Sidney Seftel, Sandra Schakowski, Pippa Skotnes, Amy Spriggs, my UWC undergraduate class, Tracey Wallace and Anat Yakuel for making my Cape Town memories all the more unforgettable.

Sheila Rock - for the colour and the smiles. Thanks Sheila!

Mark 'Phædrus' Cooper.

Justin O'Riain, Andrew Spinks and Laura-Anne van der Westhuizen - mostly for the tolerance, but also for the inspiration.

Colin, Bertrand, Stanislaw, Alan, Daniel, Douglas, but mostly Kikis, Charles, and Rudolf for the thought. Everard, Kahlil, William and John for the poetry. Tom, Nick, Bob, Ismaël, and Ludwig for the music. Club Logos for the dance. Ted and Rose for the food. Twinings for the tea. Lightspeed Inc. for the modem. Polyalphabetical ciphers for the timeless amusement.

And, of course, the Mother City with your mountains, rivers, oceans and lights.

List of Tables

Table 2.1	Results of playback experiments to males	49
Table 3.1	Literature survey of analytical aspects of vocal signatures	105
Table 3.2	Literature survey of experimental aspects of vocal signatures	111
Table 3.3	Predictor variables used in GLM analyses	116
Table 3.4	GLM result summary	117
Table 3.5	Discriminant function analysis summary (naked mole-rat)	118
Table 3.6	Standardised coefficients of DFA analysis (naked mole-rat)	119
Table 3.7	Discriminant function analysis summary (barking gecko)	120
Table 3.8	Standardised coefficients of DFA analysis (barking gecko)	121
Table 3.9	Chorus duration multiple-regression summary	122
Table 5.1	Historical taxonomic features of <i>Ptenopus</i>	162

List of Plates and figures

Plate 1.1	Photograph of study site	20
Plate 1.2	Photograph of male <i>P. kochi</i>	21
Figure 1.1	Distribution of <i>Ptenopus</i> species in southern Africa	22
Figure 2.1	Mapping of individuals in two-dimensional space	50
Figure 2.2	Histogram of squared nearest neighbour distances	51
Figure 2.3	Observed vs. random distributions of variate y	52
Figure 2.4	Bivariate kernel plot of gecko concentration on study site	53
Figure 2.5	Bivariate kernel plot of female concentration on study site	54
Figure 2.6	Sonagram of barking gecko advertisement call	55
Figure 2.7	Sound field investigation setup	56
Figure 2.8	Observed vs. expected sound pressure decay over distance	57
Figure 2.9	Frequency distribution and coefficient of variation of r'	58
Figure 2.10	Plot of residency and $rx_{(1)}$	59
Figure 2.11	Plot of $rx_{(1)}$ and adjusted residency scores	60
Figure 2.12	Frequency distribution of C_1l_x	61
Figure 3.1	Sonagram of barking gecko and call descriptor measures	123
Figure 3.2	Histogram of call click number for <i>P. kochi</i>	124
Figure 3.3	Sonagram of naked mole-rat soft chirp and descriptors	125
Figure 3.4	Canonical plots of DFAs (naked mole-rat)	126
Figure 3.5	Canonical plots of DFAs (barking gecko)	127
Figure 4.1	Three-dimensional plots of residency on burrow patterning	146
Figure 4.2	Three-dimensional plots of mass on burrow patterning	147
Figure 4.3	Three-dimensional plots of SPL on burrow patterning	148
Figure 4.4	Three-dimensional plot of mated male localities	149
Plate 5.1	Photographs of toe scaling of <i>P. kochi</i> and <i>P. garrulus</i>	164
Figure 5.1	Flow diagram of behavioural profiles in <i>P. kochi</i>	165
Figure 5.2	Sonagram of advertisement call of <i>P. garrulus</i>	166

Table Of Contents

	page
Abstract	ii
Declaration	iii
Acknowledgements	iv
List of Tables	vi
List of Plates and figures	vii
 1. Introduction	 1
1.1. Natural history and geographical distribution of the genus <i>Ptenopus</i>	 2
1.2 The study area	4
1.3 Methods of marking, measurement and observation	5
1.4 A note on statistical analyses	6
1.5 Introductory observations	8
1.6 Additional methods and materials used for this study	13
1.7 Objectives	14
1.8 Overview of dissertation	18
 2. Competition	 23
2.1 Competitive spacing	26
2.1.1 Methods	27
2.1.2 Results and discussion	30
2.2 Sound pressure	31
2.2.1 Methods and materials	33
2.2.2 Results and discussion	34
2.3 Modelling sound pressure decay	35
2.3.1 The model construct	37
2.3.2 Results and discussion	39
2.4 Playback Experiments	40
2.4.1 Playback methodology	41
2.4.2 Results	43
2.4.3 Discussion	44
2.5 Competition conclusions	46

3. Vocalisations	62
3.1 General methods and materials	65
3.2 Call correlates	66
3.2.1 How informative is between-click interval?	67
3.2.2 Peak frequency or averaged harmonic structure?	68
3.2.3 How do call duration and rate decrease over time?	69
3.2.4 Whither click number?	71
3.2.5 General call correlates	71
3.3 Information content of vocalisations : summary	73
3.3.1 Introduction to signature systems	74
3.3.2 The search for individual recognition cues	76
3.3.3 Identifying a signature	78
3.3.4 A methodological solution	81
3.3.5 The playback paradigm	82
3.3.6 Theoretical implications	84
3.3.7 A case study : the naked mole-rat and the barking gecko	85
3.3.7.1 A note on receiver psychology	87
3.3.8 Methods : generalised linear models and covariate-adjusted discriminant-function analysis	88
3.3.9 Results	91
3.3.10 Discussion	94
3.3.11 Conclusions	96
3.4 Modelling chorus activity	97
3.4.1 Model Selection : forward stepwise multiple-regression.	98
3.4.2 Results and discussion	100
3.5 Vocalisation conclusions	101
4. Sexual Selection	128
4.1 Objectives and methods	133
4.2 Correlates of mate choice	139
4.3 Discussion	142
5. Synthesis	150
5.1 The species of <i>Ptenopus</i> ?	150
5.2 Synthesis	154
References	167
Appendix I	207

SECTION 1

Introduction

The evolution of animal signalling systems - particularly of mate choice - is one of the most exciting and controversial areas in evolutionary biology (Halliday 1983, Kirkpatrick & Ryan 1991, Harper 1991, Andersson 1994). Pair-forming systems characterised by long-range male signalling and female orientation towards such signals are favoured by researchers of behavioural ecology, especially in instances where mating systems are non-resource based (Kirkpatrick & Ryan 1991). This regard is due to the potential that such systems afford for examining female choice in isolation from the effects of inter-male competition. Furthermore, owing to the advances in technology that allow for sound to be physically described, synthesised and precisely played back, a large proportion of studies have been conducted on systems of acoustic signalling. It is known that females of many species base their choice of mates principally or entirely on acoustic signals (Klump & Gerhardt 1987, Gerhardt 1988) as do males their assessment of competing conspecifics (Davies & Halliday 1978, Arak 1983, Robertson 1984, Wagner 1989). For this reason, cues in additional sensory modalities are presumably unnecessary for understanding and eliciting natural behaviour in test animals. The ability to analyse the information content of vocalisations, and to test phonotactic responses of males and females in many species of anurans and orthopterans has rendered acoustic signalling a focus for much empirical work in both communication biology and in sexual selection.

Barking geckos (genus: *Ptenopus*) are unusual animals in that they are one of the few reptiles with the ability to vocalise. They are a terrestrial genus and males have been observed calling from their burrows during the summer months. Reproduction appears to be seasonal and coincides with the hot summer months. Little is known about the biology of these animals and more specifically, the functional significance of their vocalisations. Taxonomic and some observational studies have been pursued on the genus (Loveridge 1947, Underwood 1954, Mertens 1955, Brain 1962, Haacke 1964, 1969, 1975, Bauer 1990) but no study, to date, has attempted to determine the evolutionary significance of their calls or their behaviour. This work is an attempt to initiate an experimental research program into the acoustic communication of this unique group of animals.

This introductory section provides an overview of the methods used, introduces the study site and the study population and, from the results of a preparatory behavioural period, formulates working hypotheses that form the basis for the rest of this dissertation.

1.1 Natural history and geographical distribution of the genus *Ptenopus*

In 1849, Sir Andrew Smith described a species *Stenodactylus garrulus* found in the “sandy parts of the interior of Southern Africa”. In 1865, the species *Ptenopus maculatus* from Damaraland was described by Gray, but was placed then in the family Agamidae. In the same year, Gunther synonymised *P. maculatus* with *S. garrulus*. Three years later *Ptenopus* was moved to the Gekkonidae family based on the osteological studies of Cope (1868).

Later, Fitzsimons (1935) revived *maculatus* as a subspecies of *garrulus*. This revision was supported by both Loveridge (1947) and by Mertens (1955). The two subspecies were supposed to differ in the size of the dorsal, ventral and gular scales. Brain (1962) pointed out that these characters were far too variable to be useful as subspecific characters, and he synonymised these two forms again. Brain also recognised the presence of a second

species, *P. carpi*. *Ptenopus carpi* was distinguished from *P. garrulus* predominantly on toe fringing (the toes of *carpi* were weakly fringed laterally), the number of labial scales (labials fewer in *garrulus*), and different habitat preferences (*carpi* was restricted to gravel substrates, *garrulus* to a sandy habitat).

Haacke (1964) described the presence of a third species, *P. kochi*. The fingers of *P. kochi* were fringed with elongated pointed scales, whereas the scaling on the fingers of *P. garrulus* were pointed and triangular. There was also a greater number of scales around the mid-body of *P. kochi* than in *P. garrulus*. Haacke (1964) further pointed out that each of the three species had a distinctive call, with the number of clicks in any one call being a key distinguishing feature between them. In a paper dedicated exclusively to vocalisations in the *Ptenopus* genus, the importance of call features of the three species was further elaborated upon and reinforced (Haacke 1969). The status of *P. garrulus* was revised and subspecific status was again granted to both *garrulus* and *maculatus* types based on body scale size (those of *P. g. garrulus* were smaller than *P. g. maculatus*) and patterns of colouration (Haacke 1975). No revisions to the genus have taken place subsequent to this later work (Branch 1988).

It appears that both *P. kochi* and *P. carpi* show specific habitat preferences, whereas *P. garrulus* is found over a greater range of mixed habitats. *Ptenopus kochi* is endemic to the soft sands in the river bed and the plains south of the Kuiseb river in the Central Namib desert (Haacke 1964). *P. carpi* is found only on the gravel plains north of the Kuiseb river where the substrate is relatively coarse and hard (Brain 1962). *Ptenopus garrulus* has a wider distribution throughout the drier and sandy areas of southern Africa, but is never found in softer river sediment (Gray 1865, Haacke 1975) (Fig. 1.1).

1.2 The study area

The Desert Ecology Research Unit (DERU) station is situated in Namibia at Gobabeb on the northern bank of the dry Kuiseb river (23° 34' S 14° 03' E) some 100 kms southeast of Walvis Bay and about 55 kms east of the Atlantic coast. This region may be ideal for comparative studies within the *Ptenopus* genus as both allopatric and sympatric populations of the three species occur together in close proximity to one another. All three species supposedly occur in sympatry in the Gobabeb region (Haacke 1964), albeit in different habitats. Two species are also thought to occur in various stages of allopatry in similar habitats (*P. garrulus* and *P. carpi*).

Fieldwork was conducted at DERU, Gobabeb from 10th September 1995 until 23 December 1995. This period encompassed the peak activity periods of the study animals. *P. garrulus* was observed to have been active from early September through until late December but individuals in and around the DERU station area were widely scattered, few in number and therefore less workable than *P. kochi*, which was found to occur in larger aggregated populations. *Ptenopus carpi* was not observed or heard over the study period. This study chose to focus on *P. kochi*. However, incongruous aspects of the historically noted comparative differences between the species are considered later in detail (see Section 5.1 'The species of *Ptenopus*?').

It was found that geographically discrete populations of *P. kochi* inhabited the fine sand environment of the Kuiseb river bed in the central Namib desert where individual animals occupied elaborate burrow systems (Haacke 1975). A study site (approximately 50 x 50 m) was selected where the density of *P. kochi* individuals was high, as gauged by the intensity of evening chorusing activity. In order to find such an area, several evenings were spent walking along the river bed of the Kuiseb river and the inter-dune spaces in relatively close proximity (± 1 km) of the DERU station. A suitable study site was selected at the station's southeastern periphery, against the fence (see Plate 1.1). Interestingly, this site was also the area selected by researchers the previous year (hereafter referred to as the '1994 field season'). Gecko individuals were observed to be tightly clumped around a central patch of evergreen *Acacia* vegetation.

1.3 Methods of marking, measurement and observation

Individual animals were caught by means of a small noose hung over the burrow entrance. This noose was tightened once the animal had protruded its head through it. Captured animals were toe-clipped for permanent identification, and numbered with a permanent marker pen on the top of their heads for short term (week by week) visual identification. Toe-clippings were preserved in 70 % ethanol for later examination. Individuals were also sexed and measured. Snout-anal-tail length (length), and the extent of yellow colouration (measured from the apex of the rostrum anteriorly to the base of the gular folds posteriorly) were measured with a vernier calliper to the nearest 0.1mm. An Ohaus portable scale was used to measure mass to the nearest 0.1g. Sound pressure level (SPL) was measured with a Realistic Sound Level meter on fast setting. Filtering methods for measuring SPL, the logarithmic nature of the decibel scale and SPL averaging are dealt with fully in Section 2.2.1. Sound recording methods are dealt with in detail in Section 3.

Within the first six weeks of the study period, 50 burrows were marked and identified by pushing stakes in within five cm of each burrow's entrance. Each stake was numbered and reflective tape attached to its apex. Burrow staking was conducted during the mid-day when gecko activity was absent. Non-intrusive observations were made every evening from dusk until well after sunset with the aid of a head-mounted torch covered with a red filter. Individual animals were easily located in the evening owing to the reflective properties of their eyes. Furthermore, reflective banding on the numbered stakes provided a good proximate mapping of the gecko sites when available light was low. Sudden torch movements while observing geckos were avoided.

In the summer of 1994, a preliminary investigation was initiated in an attempt to begin researching aspects of the breeding behaviour of two of the sympatric species of *Ptenopus* - *P. kochi* and *P. garrulus*. Marshall was the field investigator, and he courteously provided his unpublished data to aid the ongoing *Ptenopus* investigations. These 1994 field observations are compared with the 1995 field season data (see Section 1.5).

1.4 A note on statistical analyses

This research makes use of a range of statistical methodologies and techniques, many of which are repeated throughout various sections of this dissertation. When specific techniques or particular experimental designs are used in any one sectional investigation, these are described *in situ*. All other general techniques are noted here for brevity sake and for interpretational clarity.

Parametric tests are used when the variable(s) do not differ significantly from a normal distribution. The Kolmogorov-Smirnov goodness-of-fit test was used for assessing significant departures from normality (Neter *et al.* 1988). To assess the relationship between two global variables, the Pearson product moment correlation was used (Zar 1984). The strength of this relationship is indicated by the magnitude of the correlation coefficient r (where r is 1 : perfect positive relationship; $r = 0$: no relationship; $r = -1$: perfect inverse relationship) and by the probability level P . Where one variable can be considered a continuous response variable, and the other a continuous independent variable, least-squares regression was used (Zar 1984). Here, the R^2 statistic is used to describe the percentage of variation of the response variable that can reliably be accounted for by its covariation with the independent variable. Multiple regression was used when there were several independent variables (Belsley *et al.* 1980). All regression output was analysed for significance using analysis of variance (ANOVA) procedures. Two-sample tests of significance of parametric data are analysed using Student's t -test, or a paired sample t -test where the data consist of repeated measures (*sensu* Hand & Taylor 1987). ANOVA techniques are used in testing for significant factorial-level partitioning of the variance associated with a response variable and two or more levels. Model I (random effects) and model II (fixed effects) one-way and two-way ANOVAs, and Model I and Model III (mixed effects) multifactorial ANOVAs were used (Neter *et al.* 1988). Analysis of covariance (ANCOVA) procedures are used to control for the covariance between a response variable and an independent factor (Sokal & Rohlf 1981).

Where data did not conform to the assumption of normality, nonparametric procedures were used (Siegel and Castellan 1988). This occurred when the data set was too small to test for normality, when the data could not be adequately transformed to normality, or when transformed data continued to display heteroscedascity (unequal variances). Spearman rank-order correlation was used to assess the relationship between two global variables. The correlation coefficient - r - is similarly interpreted as the Pearson r (see above). Two-sample data were tested for significant differences in the distribution of their rankings using the Mann-whitney U test. U statistics were adjusted for tied ranks if they were present (Kendall 1962). Where the two sample data was paired, Wilcoxon's matched-pairs test was used. Multisample testing of nonparametric data was conducted using the Kruskal-Wallis ANOVA analog. Chi-square analyses are used for testing of significant differences between categorical frequency data. The binomial exact test was used for assessing significant departures of Bernoulli trials from random.

All suitable data were first tested for normality and for equality of variances (variance ratio test) before subjecting the data to parametric analyses. Unless otherwise stated, the results of these preparatory tests are not usually presented when inductive parametric statistics are used. All data transformations are, however, noted in the text. Unless indicated, all parametric results have been checked for homoscedacity in the residual scatter. One-tailed tests are used when *a priori* evidence or logic predicts directionality of the test response and are noted in text when used. All other tests are two-tailed. The alpha level of significance was set at 0.05 for all tests. Where heavy reliance is made on the inductive inference of a biologically useful probabilistic explanation (*sensu* Hempel 1966) in a sequential test, probability levels are adjusted (indicated by P_{adj}) using Bonferroni procedures (Rice 1989).

1.5 Introductory observations

Preliminary behavioural observations (1995 field season)

Preliminary studies were conducted in order to be able to formulate testable hypotheses (see Section 1.7). For these studies, on-site behavioural observations were made over 104 evenings. Active chorusing activity occurred on only 74 of these evenings. Hence, 29 % of the nights were silent.

The population of *P. kochi* at the study site was comprised of four classes of individuals : resident calling males, resident non-calling adult males, resident adult females and juveniles (individuals too small to be sexed). Males were identifiable by a bright yellow throat (Plate 1.2). The activity cycle of this species is typically crepuscular, with calling males chorusing at dusk (sunset + 20 minutes) and dawn for a average duration of 57 and 10 minutes respectively. Males called from one of several self-constructed burrow entrances in his immediate vicinity.

During the active season, 7-15 males were found to be vocalising on any one night at the study site. On hot evenings, females and non-calling males would leave their burrows and forage under the nearby vegetation on a mixture of termites, ants, small beetles and moths. Here, individuals were found within centimetres of one another. No agonistic non-calling male-female, or female-female interactions were witnessed.

Interestingly, calling males, for the duration of their tenure at a calling site, were never seen to leave and forage. They did, however, infrequently prey on insects that came within a few centimetres of their burrow entrances. Males often disappeared from a calling site for one to three weeks or sometimes permanently. Whether they left the site completely, or remained underground during this period is not known, but individuals reappearing after such an absence had often put on substantial weight, and had lost their ink markings, presumably through moulting. However, males need not have given up burrow tenure to moult as calling males were frequently caught that were well into the process of moulting.

It is probable that these absentee males left their burrow system to forage elsewhere, eventually returning, often to their original sites, to resume calling.

Twenty-eight adult resident individuals were noted from the study site. This group consisted of five females and 23 males and represents the total gecko population in the study area. Five juvenile individuals were noted, but these were too small to be sexed. On average, only 14 adult males occupied the site at any one instance, most of which would be vocalising at any one time.

Turnover in callers was high. Of 23 individuals caught in the confines of the study area, only six were identified as having been previously toe-clipped from the 1994 field season. The within-site recapture rate is estimated at 26 % between seasons. A crude estimate of yearly turnover is estimated as 74 % (i.e. approximately 3/4 of once-marked males had vanished from the study site). This seemingly excessive turnover rate does raise serious questions as to the presence of a sampling artifact being introduced into the study due to the inherently intrusive marking methods. However, five other clipped males from the 1994 field season were found further afield (within 300 meters from the study site area) while I was randomly sampling calling males outside of the study area. It is unlikely, therefore, that individuals suffered increased mortality as a result of the marking protocol, although investigations into a potential causal link between marking and increased dispersion would be useful if more certainty could be placed in the population trends observed here. Within the 104 day study, of the 23 individual males marked and observed, 15 had disappeared. The turnover rate of breeding males averaged 16 % per month.

On a day-to-day scale of analysis, it was apparent that the barking gecko system is dynamic. Each caller utilises from one through to seven different burrow entrances, and these are connected underground. Normally, one entrance is selected for any one night of chorusing, but it is not unusual to see a calling male running from one entrance to the other, or diving into one burrow and reappearing at other entrances. The frequency of burrow swapping from night to night was clearly enhanced by the disturbance of playback experiments (see Section 2). Interestingly, with all this moving about, calling males sometimes ventured too close to each other - and one of several things was observed to

happen. First, one of the males left the burrow entrance that he was advertising from and reappeared in another of his burrows further away from the rival's sound source. Second, the males became vigilant (ceased calling, and extended their heads a considerable way out of their entrance) and then responded antiphonally to their neighbours' calling. Lastly, males sometimes charged (attacked) their neighbours (although charging has been witnessed, actual fighting has not been). These observations suggest a possible role, for some acoustic characteristic of the gecko vocalisation, that is dependent on distance, mediating the establishment and maintenance of territorial spacing.

Interestingly, in a few observed instances, a male vacated his calling site area (within 2 m) and it was rapidly taken over by a new (previously unmarked) male. One inadvertent removal experiment showed that in just one night a new male commenced calling in the area where the previous resident had been calling.

In 1994, Marshall (unpublished data) documented the presence of five adult *P. garrulus* sharing the study site where *P. kochi* were calling. Upon inspection of the toe-clippings of these animals, it was clear that *P. garrulus* had been misidentified, and was actually *P. kochi* (see Section 5.1). The vocalisations of several of these individuals were also recorded in 1994, and sonographic analysis substantiated this identification error (see Section 3.2).

The average operational sex ratio for the 1995 study was estimated as 0.36 females : 1 male. Marshall reported the presence of 48 residents, six of which were juvenile males, 19 adult males, 20 adult females and three juvenile individuals. The permanence of these individuals (specifically males) was not noted, and an operational sex ratio cannot rightly be calculated.

Mating Behaviour

Non-calling males and females strictly avoided the 'active' spaces of vocalising males, except on rare occasions when females wandered around these areas, approached one to several calling males, sampled different burrow systems (entered a burrow, reappeared seconds later and moved off), and eventually stayed in the burrow of a chosen male. This behaviour occurred well into hot evenings. Upon being approached by a female, a barking male would

leave the burrow entrance and approach the wandering female. He would emit a mating gurgle (a low intensity, monotonous series of rapid clicks) and disappear head first into the burrow followed by the female. Similar gurgle vocalisations were heard from deep inside the burrow, and later the female sometimes reappeared at an alternative burrow entrance and left. Alternatively, she remained with the male from a few days or up to three months (sample size = 3 observed matings, in addition to 3 observed associations at the beginning of the 1995 field season). During this time, females were witnessed to leave the burrow system and go foraging. Interestingly, near the onset of the study, several males were observed having two females associated with them. The nature of the female wandering from burrow to burrow, and eventually choosing a mating residency with a calling male suggests an active role in female discrimination (*sensu* Arak 1988).

Juvenile individuals (less than 4 cm in length) were observed emerging from the burrow networks of calling males at the very beginning (early September) and also towards the end (mid-December) of the field season. These juveniles remained residents for a few days to several weeks, and then disappeared.

Morphological measures

Morphological (including yellow colouration and SPL) intercorrelations are analysed using 1995's data. During the 1994 field season, Marshall (unpublished data) identified 48 individuals and data were collected on length, mass, yellow (if male), and sex (if sexable) for most of these individuals. Marshall noted only three individuals that he claims to have been unsexable, as juveniles. These unsexable individuals were smaller than 7.5 cm in length and weighed less than 1.6 grams. Several aspects of Marshall's 1994 data were used for comparison with the data from the present (1995) study. The differences in masses and lengths of adult males and adult females from the 1994 data set are investigated. Second, morphology (including colouration) of adult males is compared between the two field seasons. Lastly, differences between adult male callers and non-callers are investigated within and between the two field seasons. Summary statistics (mean, standard deviation, sample sizes etc.) of all measures are presented in Appendix I.

Examination of the 1995 morphological measures of 23 individual males shows that except for the relationship between length and yellow (Pearson product moment correlation : $r = 0.402$, $P = 0.123$), significant collinearity exists between measures of length, mass, yellow and SPL (mass/yellow : $r = 0.698$, $P = 0.003$; mass/length : $r = 0.518$, $P = 0.040$; mass/SPL : $r = 0.760$, $P = 0.001$; yellow/SPL : $r = 0.649$, $P = 0.007$; length/SPL : $r = 0.560$, $P = 0.024$)

Inspection of the 1994 data reveals that there were no significant sexual differences between the mass or length measures of individuals (Student's t test : mass : $t = -0.802$, d.f. = 37, $P = 0.427$; length : $t = -0.636$, d.f. = 37, $P = 0.529$). When the 1994 and 1995 data of adult male morphology were contrasted, no significant differences between the three morphological measures were found (Student's t test : length, $t = 1.212$, d.f. = 40, $P_{adj} \geq 0.60$; yellow, $t = 1.475$, d.f. = 40, $P_{adj} \geq 0.30$; mass, $t = 2.140$, d.f. = 40, $P_{adj} \leq 0.15$).

Lastly, differences in morphology between callers and non-callers were contrasted using the 1994 data (six male non-callers, 19 calling males). Significant differences were found in both length and mass (Mann-whitney U test : length : $U = 109.000$, d.f. = 1, $P_{adj} = 0.003$; mass : $U = 102.000$, d.f. = 1, $P_{adj} = 0.016$) but not in yellow gular colouration ($U = 93.500$, d.f. = 1, $P_{adj} = 0.057$). No morphological differences were found to exist between non-callers of the 1994 and the 1995 seasons (length : $U = 0$, d.f. = 1, $P = 0.127$; yellow $U = 0.500$, d.f. = 1, $P = 0.199$; mass $U = 0$, d.f. = 1, $P = 0.30$).

Taxonomic placement of *P. kochi* based on behavioural observations

There have been two main types of mating system described for lizards : polygynous and promiscuous. These two systems have been closely associated with foraging mode (Stamps 1983a) : sit-and-wait feeding versus active foraging. Lizards exhibiting sit and wait strategies tend to be territorial. It has been shown that these lizards exhibit polygynous mating systems with long-term pair bonds (Trivers 1976, Ruby 1984). Conversely, actively foraging lizards rarely defend any of their home range and the mating associations between males and females in these species is brief, lasting no longer than copulation (Carpenter 1960, Andersson & Vitt 1990).

Ptenopus kochi seems to be anomalous in these respects. The observational studies on chorusing behaviour of *P. kochi* suggest that males are strongly territorial. Interestingly, individuals of *P. kochi* exhibit both types of foraging strategies depending primarily on their gender, and presumably their physiological state, if male (see Section 4). Females actively search for food, while displaying males adopt a sit-and-wait feeding strategy. Other males, are significantly lighter and shorter than the displaying males, and forage alongside females. Mating associations in *P. kochi* appear to be prolonged, and polygyny has been observed.

In most reptiles, females are larger than males (Shine 1978, Berry & Shine 1980). This is commonly attributed to the fitness advantages of increased fecundity since fecundity is often proportional to body size (Trivers 1972, 1976). However, males are reported to be larger than females in most lizard species (Stamps 1983a). The present study shows no significant differences in the three phenotypic measures between the sexes.

1.6 Additional methods and materials used for this study

Evening chorus behaviour commenced approximately 20 minutes after sunset, escalating from a few isolated calling individuals to alternating vocal activity involving most males in the study area. Chorus activity typically lasted one hour, and thereafter decayed in magnitude to where only isolated individuals could be heard calling infrequently. In order to quantify chorus duration accurately, a threshold value for the number of calls heard in the study area needed to be established. Choruses were considered to have started when one or more vocalisations emanated from the study area every minute. Choruses were considered to have ended when the call rate of the chorus dropped below this level. Chorus duration is explored in Section 3.4 (Modelling chorus activity).

The tenure of a calling individual's residency in a specific burrow area (hereafter referred to as 'chorus site tenure') was often sporadic. In an attempt to quantify features of this temporal variation of individual male's persistence in the chorus, each individual's tenure was noted throughout the study period and rankings were assigned towards the end

of the study period to what appeared to be generalisable trends in residency behaviour. A ranking of '1' was given to individuals whose tenures were ephemeral. These individuals were observed to have been active participants for several days to two weeks. Thereafter, these individuals disappeared and were not observed calling again within the study site. Rankings of '2' applied to individuals who sometimes disappeared from a calling site for one to three weeks, but who always reappeared thereafter (most often in close proximity to their past burrows). A ranking of '3' was assigned to individuals who were never observed to have left the chorus area for longer than a week. These individuals were the most permanent chorus residents over the study period. Residency rankings are analysed in Section 2.3 (Modelling sound pressure decay) and in Section 4.2 (Correlates of mate choice). It is interesting to note here that of the six males recaptured from the 1994 field season, four of these displayed high levels of chorus site tenure during the 1995 field season (i.e. residency rankings = 3).

Burrow activity was checked twice weekly throughout the initial six week period for each of the 50 staked burrow entrances (see Section 1.3). Burrow activity was indexed by assigning a character state to the activity level of the burrow entrance - open, closed or active (calling male present). Burrow activity is investigated in Section 4.2 (Correlates of mate choice).

1.7 Objectives

This vigorous preparatory study yielded some interesting clues as to the significance of calling behaviour of *P. kochi*. The behavioural information forms a favourable basis for generating several explicit working hypotheses. Several of these are tested in an attempt to understand the biological significance of aspects of vocalisation in *P. kochi*. The bases for these hypotheses are discussed below.

Competition

The vocal behaviour of *P. kochi* is crepuscular. Such concentrations of signalling within a restricted time interval usually occur close to photoperiodic transitions, and similar incidences of collective displaying has been documented (cicadas : Young 1981; birds : Kacelnik & Krebs 1983; anurans : MacNally 1984; grasshoppers : Greenfield 1992). Furthermore, the acoustic signals produced by *P. kochi* exhibit collective patterning of temporal signal interactions, where vocalising males alternate their acoustic interactions with neighbouring males thereby avoiding call overlap. The possible adaptive and non-adaptive explanations for this type of acoustic interaction are reviewed by Greenfield (1994). Several hypotheses have been forwarded to explain the function of call alternation in anurans (see Schwartz 1987). Individual males may be cooperating in achieving and maintaining particular phase relationships for several reasons : the male-male interaction hypothesis suggests that call alternation serves to maintain the acoustic space between males. Acoustic overlap is thought to impair an individual's ability to estimate the intensity of his neighbour's call and to maintain inter-male spacing. Second, the temporal information hypothesis argues that call overlap will corrupt any temporal information used by females to discriminate between males. Lastly, call overlap will make localising a sound source hard for prospecting females (the auditory masking hypothesis). It appears that while the auditory masking hypothesis is not well supported by experimental fieldwork, the first two hypotheses explain call alteration in certain anurans (Schwartz 1987, Schwartz & Rand 1991). While study into the temporal aspects of these interactions are necessary for a better understanding of the bases of sexual selection (e.g. Simmons & Zuk 1992, Jennions *et al.* 1995), female preferences for call alternation patterns were not investigated in this research.

An advertisement call may indicate the position of a male to its neighbours (as implied by the male-male interaction hypothesis), and several researchers have shown, by playing back tape-recorded calls, that vocalisations elicit territorial behaviour and thus play a role in inter-male spacing (Robertson 1984, Wilczynski & Brenowitz 1988). Many studies on acoustic communication in anurans have implicated the intensity of the sound in advertisement calls in the evolution and maintenance of breeding territories (Brenowitz *et al.* 1984, Telford 1985, Gerhardt *et al.* 1989). The possibility that spacing is acoustically mediated is tested and several of the experimental paradigms used in studies of acoustic

communication (e.g. playback experiments) are adopted in an attempt to better understand the mechanisms behind territoriality in barking geckos.

It is also possible that signal interactions between males of *P. kochi* facilitate assessment on an individual level. Agonistic encounters were observed when calling *P. kochi* males ventured too close to one another, suggesting a possible role for the vocalisation in inter-male assessment as well as in the maintenance of inter-male spacing. Mutual appraisal is thought to be advantageous when contests are costly (Harper 1991). In many lizard species, differential fighting ability often translates into either holding a territory (Hews 1990) or holding a larger territory (Trivers 1976, Ruby 1984). This then translates into priority mating success (Censky 1995). The nature of asymmetry between *P. kochi* males in contests for acoustic territories is investigated, as is the role of prior territory ownership as a principal determinant of the payoff asymmetry between males.

The information basis of vocalisations on which male-male assessment might occur is examined. It is recognised that many elements of the behavioural repertoire of ectotherms are likely to be dependent on temperature (Willmer 1991). It is therefore of interest to understand how features of an individual's vocalisations predictably covary with both extrinsic and phenotypic sources of variability. The theoretical difficulties and challenges of examining differences in call characteristics between individuals are explored.

Intersexual selection

The parallels between the landmark (i.e. vegetation) based mating system of *P. kochi* and lek mating systems are immediately apparent. Both show an area of localised male aggregation, defence by males of relatively small territories and mate choice by females (Bradbury 1981). However, the leks of birds and mammals are also characterised by an absence of male parental care and an absence of any male-defended resources (e.g. food, oviposition sites, resting sites). Although the gecko system might superficially resemble a lek system, the observation that a female - once having selected a mate - lays her eggs in the male's burrow, and remains in that burrow system for an often lengthy period of time, suggests that the burrow itself may be a resource that is being offered by vocalising males to prospecting females. Furthermore, the observation that newly hatched individuals remain in

their natal (father's) burrow for a period of time before dispersing may indicate some (albeit indirect) selected form of parental care.

Intrasexual competition among males is known to be an important determinant of mating success in lizards (Tokarz 1995). Much less is known about the role that the mate choice (intersexual) component plays in determining male and female mating success, although female mate choice for display behaviour of *Anolis* lizards has been demonstrated (Jenssen 1970, Crews 1975, Sigmund 1983, Fleishman 1992). Females may choose males strictly on the basis of some feature of their phenotype or behaviour (Halliday 1983). Females may prefer males with particular behavioural repertoires, and several models of sexual selection suggest that males with elaborate or prolonged courtship displays could be indicating their quality to females (Kirkpatrick & Ryan 1991, Maynard Smith 1991). Implicit in all these concepts is the assumption that displays are costly: opponents and potential mates can only assess male quality if only males of high quality are better able to support display costs (Zahavi 1975, Grafen 1990, Maynard Smith 1991, Johnstone & Grafen 1992, Hutchinson *et al.* 1993). The advertisement or mating calls of male animals (especially anurans) have often revealed a role in conspecific mate attraction, and these calls may be used by females to assess the quality of vocalising males as potential mates (Halliday 1983, Gerhardt 1988). Similarly, *P. kochi* females have the opportunity to assess directly the phenotypic qualities of males holding particular territories because males have presumably established their territories before the females become sexually receptive.

Fundamental to sexual selection theory is the notion of fitness trade-offs in traits that are subject to both sexual selection and natural selection. The study of energetic costs and constraints to mating behaviour thus forms a central theme of investigations in sexual selection and mating display behaviour patterns have been shown to be energetically costly in several species on a short-term basis (reviewed in Halliday 1987, Vehrencamp *et al.* 1989). The high energetic costs of vocalising and territorial maintenance in anurans (MacNally 1981, Ryan 1985, Taigen & Wells 1985, Wells & Taigen 1989), in combination with reduced foraging opportunities (Woolbright 1985, Woolbright & Stewart 1987) have been related to the observation that in many species of anurans with prolonged breeding, individuals often vary their activity levels each night and the duration of their tenure in a

chorus. The division of foraging budgets between calling male *P. kochi* and non-callers, and the exclusive and often sporadic chorus site tenure of calling males in the chorus suggests that vocalising in *P. kochi* is energetically expensive. In addition, the fact that non-calling adult males tended to weigh significantly less and were shorter than calling males suggests strongly that some aspect of condition reliably distinguishes these two classes from each other. Accordingly, energetic aspects of chorusing activity are investigated.

Females may also simply base their mating preferences for particular males on the quality of a male's resources rather than directly on any male phenotypic characters (Emlen & Oring 1977, Halliday 1983, Partridge & Halliday 1984, Maynard Smith 1987, Davies 1991). In resource-based systems, the immediate benefit that males contribute is often cited as the evolutionary basis for female choice (e.g. oviposition sites in bullfrogs, Howard 1978; nuptial gifts of prey in scorpionflies, Thornhill 1981). Females should prefer males offering superior resources, and presumably choice has evolved because superior resources confer increased reproductive success (Thornhill & Alcock 1983). In so far as male lizards do not offer direct parental care or food to prospective mates, female preference for resources, if present, would be based on the quality of resources within a male's territory (Andrews 1985). Correlates of mating success in *P. kochi* are investigated, and the issue of whether female *P. kochi* choose where to mate, based on the availability of some resource on a male's territory or solely on some male phenotypic trait, is debated.

1.8 Overview of dissertation

Section 1 (Introduction) dealt with the introduction to the genus *Ptenopus* and to the general field and statistical methods. It also examined behavioural observations of *P. kochi* and discussed the objectives for the rest of the study.

Section 2 (Competition) looks at aspects of competition in *P. kochi*: how calling males are distributed relative to one another and the evidence for regularity of spacing in dense aggregations. Sound intensity is investigated as the mechanism of this spacing. Sound intensity is mathematically modelled to gauge whether the sound intensities of nearest

neighbours overlap at similar levels and to investigate correlates of each individual's shared acoustic space. The intensity values of the observed overlap are used in a set of playback experiments. The importance of residency is also discussed.

Section 3 (Vocalisations) looks in detail at the inter-relationships between call features of *P. kochi*'s vocalisation, and how these features are related to both intrinsic (morphological) and extrinsic (ambient) sources of variability. The principles of information theory and individual recognition by voice are used to gauge the variation manifest in the features of *P. kochi*'s call. A novel statistical method for disentangling the influence of incidental sources of variation from 'signal' features in animal voices is developed, and applied in a case study to the soft-chirp of *H. glaber* and the advertisement call of *P. kochi*. Lastly, chorus duration is statistically modelled to see whether it too predictably covaries with meteorological variability.

Section 4 (Sexual selection) looks at mate-choice in *P. kochi* from a purely correlational approach. Here an attempt is made to understand how and why male gecko behaviour has evolved. The relationship between mating success, morphology and burrowing activity is explored, together with the energetics of chorusing activity.

Section 5 (Synthesis) is a synthesis of the findings of section 2 through 4, and also looks at the current taxonomic status of the *Ptenopus* species in the light of the material presented in the other sections. Some prospects for interesting future research are also suggested.



Plate 1.1 A photograph of the study site area. Gravel plains are in the immediate foreground, and the central Namib sand sea in the background. *Ptenopus kochi* inhabits the fine sand environment of the vegetated dry Kuiseb river bed.



Plate 1.2 A photograph of a male *P. kochi*.

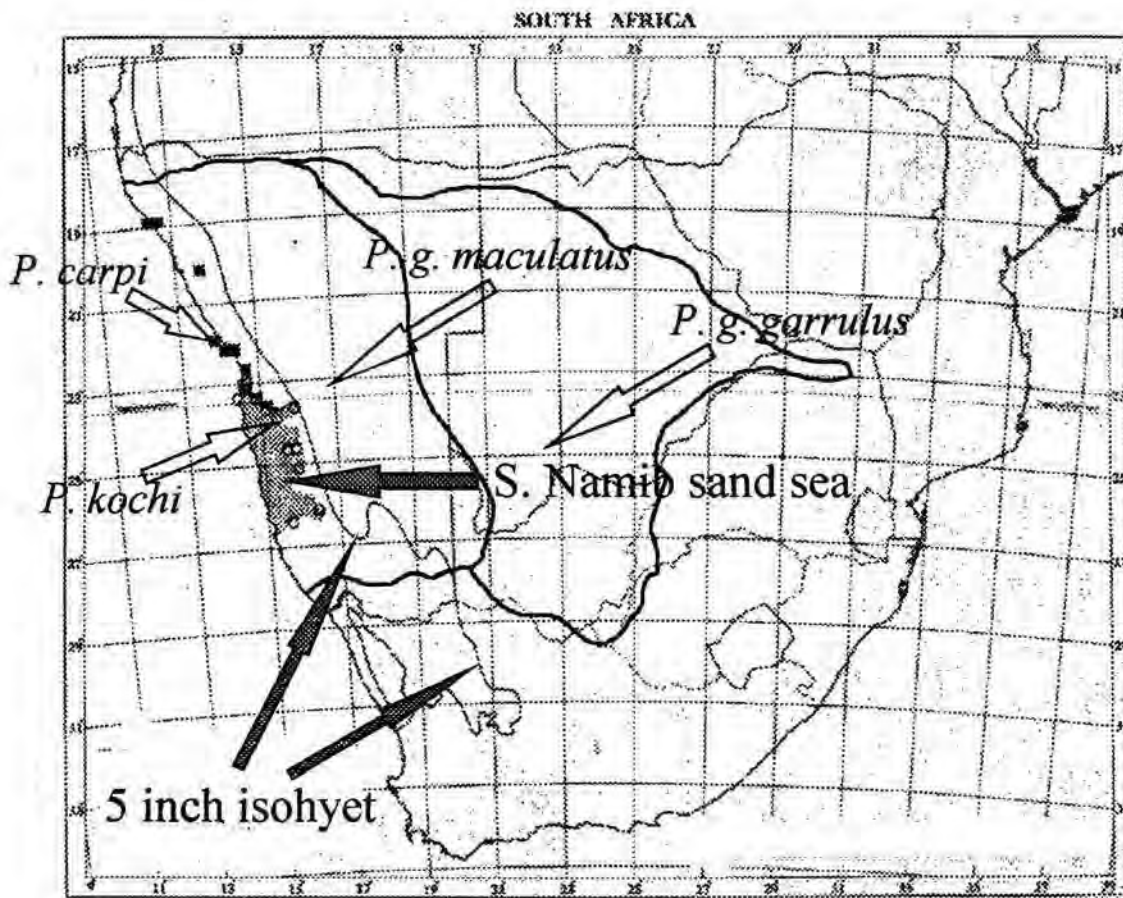


Fig. 1.1 The distribution of the three species of *Ptenopus* over southern Africa. The 5 inch (125 mm) rainfall isohyet is indicated, as is the Southern Namib desert. Arrows are for point localities for *P. kochi* and *P. carpi*, and general distributions for the two subspecies of *P. garrulus*.

SECTION 2

Competition

Territoriality occurs when an animal defends an area against others, thereby gaining increased access to resources (Kaufmann 1983). However, the delimiting constraints of this definition become apparent in the face of detail, largely because it is not altogether clear what constitutes defence, or what constitutes a resource. Most authors have persisted with some variation on the 'defence of resource' theme (e.g. Brown 1964, Baker 1978, Clutton-Brock *et al.* 1982, Warner 1990), whereas others have preferred to define territoriality in terms of whether animals are spatially patterned more than expected from a random distribution on suitable habitats (e.g. Davies 1978, Thiele & Bailey 1980, Robertson 1984, Dyson & Passmore 1992). Students of the 'defence of resource' school of thought focus attention on the behavioural processes of territoriality, while the 'distribution patterning' school are concerned with the ecological patterning that such behaviour produces. Both aspects should be viewed as essential to a comprehensive understanding of territoriality in any system, and hence a combined approach is adopted for the purposes of this study.

Competitive and territorial behaviour is common among reptiles and has been recorded in crocodiles, snakes and in lizards (Cloudsley-Thompson 1972, Schoener 1977). Social organisation resulting from aggressive interactions is characteristic of the Iguanidae, Agamidae and the Gekkonidae (Carpenter 1967, Rand 1967, Stamps 1977, Frankenberg 1982). Gekkonid lizards are known not to guard their eggs, nor do they exhibit parental

care of their young (Kluge 1967). However, studies have documented territorial behaviour in these animals (e.g. Frankenberg 1982) and experimental investigations have provided evidence for the vocal displays of male geckos functioning in the establishment and maintenance of territories (Marcellini 1977).

It is understood that when some important resource is not distributed uniformly in space, there will be an increased opportunity for resource monopolisation (Emlen & Oring 1977, Milinski & Parker 1991). Populations of Koch's barking gecko, *P. kochi*, are found aggregated among patches of *Acacia albida* in the dry river sediment of the Kuiseb river in the Central Namib desert. Each individual gecko resides in a self-constructed network of burrows. Males and females appear spatially distinct, except when sexually receptive females venture into the advertisement domain of calling males to mate and lay eggs. Individual males are faithful to a specific set of burrows, although the extent of site tenure is variable (Section 1). There is also a visible division in the foraging budgets of the gecko sexes - males adopt a sit-and-wait strategy during their chorus tenure, and rarely feed. Conversely, females position their burrows close to the tree under-litter and spend warm evenings foraging there.

Female reproductive success is known to be limited by resources and it is expected that female spatial patterning will be dependent on resource dispersion (i.e. food). Male reproductive success will be limited by access to females, and the patterning of *P. kochi* males may simply mirror female demands. It is not clear as to whether male burrows are a defended resource *per se*, or whether the distribution of males depends primarily on the spatial patterning of females (*sensu* Emlen & Oring 1977). During the 1995 field season, the operational sex ratio in the barking gecko system - defined as the average ratio of fertilizable females to sexually active males at any given time (Emlen & Oring 1977) - was heavily male biased (Section 1). The continuous long periods of sexual activity by males, coupled with brief and asynchronous periods of receptivity by females during the breeding season produces an extreme level of skew in the operational sex ratio of the barking gecko system. This imbalance creates a high degree of variance in reproductive success amongst males, and male competition for mates is intense. Conspecific gravid females are attracted

to choruses and it appears as though mates are actively chosen from within the aggregation (see Section 4).

There are several plausible hypotheses for the adaptive value of an aggregated male mating system (Davies 1991). These range from the idea that such aggregations arise when males cannot economically defend either the females themselves or the resources they require (Emlen & Oring 1977) to ideas that females prefer aggregations for improved predation defence (Gosling 1986) or for an improved range of mate choice (Trivers 1972, Williams 1966). Groups of displaying males may also have a greater attractive pull than lone displaying males (Alexander 1975, Parker 1978). There is some evidence in favour of each one of these hypotheses, but a persuasive general causal explanation for the evolution of such a mating system is still lacking. An explicit understanding of the factors governing the formation of barking gecko aggregations would require carefully designed experimental manipulations of resources or of females to provide convincing evidence that shows how female dispersion leads to male aggregation (see Davies 1991). Investigations of this type were not undertaken here.

There are a range of questions that can be posed about the causal mechanisms that govern male-male competition in *P. kochi* choruses. The spatial distribution of males within a chorus is expected to be influenced by several potential costs and benefits to mating success. Within the chorus, neighbouring males are known to present the greatest threat to any individual male's ability to attract a searching female; these immediate neighbours may mask his calls with their own (Baker 1983, Greenfield 1994). The advantages of congregation might be offset, to a certain extent, by the advantages to males of maintaining a certain degree of spacing between them and thus remaining acoustically distinct. Understanding more about these constraints and advantages may help to explain the adaptive value of male chorusing behaviour.

Mertens (1946) was the first to suggest that the vocalisation of *Ptenopus* was involved with defining a territory. Haacke (1974) reported that chorusing males spaced themselves out in the breeding area. Robinson & Haacke (1977) suggested, based on a series of observations, that the call of *Ptenopus* species probably functions to exclude male

conspecifics from the space adjacent to the burrow. The observational studies of Section 1.5 revealed how, when a calling male is approached by another vocalising male, the resident male displays vigilant or aggressive behaviour.

The understanding that both vocal interactions and offensive behaviour regulate the dynamics of inter-male spacing in anurans has long been recognised (reviewed first in Wells 1977, 1988). Studies in several frog species (*Hyla regilla*, Whitney & Krebs 1975, *Uperoleia rugosa*, Robertson 1984, *Eleutherodactylus diastema*, Wilczynski & Brenowitz 1988, *Hyperolius marmoratus*, Dyson & Passmore 1992) have demonstrated that males space non-randomly in choruses. It is understood that for a spacing strategy to be effective males must have some reliable mechanism for judging the distance to neighbouring conspecific competitors. Several studies have shown that the amplitude of neighbouring frog's calls serves as a cue for spacing within choruses of different species (Brenowitz *et al.* 1984, Robertson 1984, Telford 1985, Wilczynski & Brenowitz 1988, Gerhardt *et al.* 1989). Sound pressure level (SPL) has thus been identified as a widespread mechanism for spatial organisation in anuran choruses.

The chorusing dynamics of *P. kochi* displays striking convergences with anuran communication systems, and there is a possibility that a similar mechanism for acoustic spatial organisation exists in the gecko system. This section is aimed at investigating aspects of competition in *P. kochi*. The spacing of individuals is described in a natural breeding population using nearest neighbour analysis (Section 2.1). The hypothesis that spacing is vocally-mediated and that chorusing males gauge the proximity of neighbours through the intensity of their perceived signals is tested experimentally (Section 2.4).

2.1 Competitive spacing ?

Spacing mediated by competition implies that in a homogenous habitat equal competitors should be regularly distributed (Fretwell 1972). Such patterning is uncommon in nature though. Usually, it is found that organisms are clumped, and there are large unoccupied

areas between aggregations (Goodall 1952). Within aggregations the distribution of individuals may be regular because of the interactions between them. Consequently, a nearest neighbour analysis of the whole population will usually only detect the clumped distribution.

An analysis of distribution within an aggregated clump usually requires an arbitrary demarcation of their boundaries. Here, a technique developed by Pielou (1962) is useful in that it can detect regularity between individuals regardless of the distribution pattern of the population as a whole. This technique does not therefore require a definition of the boundaries of the clumps or of their density (c.f. Thiele & Bailey 1980).

The spatial relations between individual *P. kochi* are analysed by mapping individuals in two-dimensional space and then subjecting this patterning to several levels of analysis. Pielou's (1962) method testing for the occurrence of regularity (interaction) within the chorusing male aggregation is performed using nearest neighbour measures. Lastly, spatial aspects of chorus patterning are examined graphically.

2.1.1 Methods

In order to map spacing patterns and nearest neighbour distances between individual geckos (of both sexes) in the study population, the spatial distribution first needed to be determined. The method of least-squares mapping (Rohlf & Archie 1978) was used to map the relative locations of all burrows as points in two-dimensional space. This method is based on a least-squares estimate of the coordinates of any burrow using the observed distances between burrows, rather than triangulation methods.

The positions of burrows were marked with numbered stakes pushed into the ground within 5 cm of each burrow entrance. All visible burrow entrances were pegged and numbered in the first week of the study period during the midday, when gecko activity was absent. Distance measurements were made with a tape measure to the nearest 1 cm. First,

two burrows were selected as the base references ($x_1 = y_1 = 0$) and the distance between them was measured ($x_2 = d_{12}$). Next, the distance between these burrows and a nearby burrow (i) was measured noting which reference burrow was to the right (k) and which was to the left (j) of an observer standing at the new burrow and facing towards the previous burrows. This process was continued whereby the distances from a new burrow to two previously recorded points were recorded. The coordinates of each point (x, y) was simply reconstructed using the law of cosines, because each point is at the apex of a triangle for which the lengths of all three sides are known. The coordinates x and y of point i are

$$x_i = x_j + d_{ij} (\cos \theta)$$

$$y_i = y_j + d_{ij} (\sin \theta),$$

where

$$\theta = \tan^{-1} \frac{(y_j - y_k)}{(x_j - x_k)} - \cos^{-1} \frac{(d_{ji}^2 + d_{jk}^2 + d_{ki}^2)}{(2 d_{ji} d_{jk})}$$

Coordination approximation errors tend to accumulate using the above method because computation proceeds following the stepwise fashion in which the different burrow localities are recorded. The internal consistency of burrow positions was therefore cross-validated by taking several additional measurements of distances between pairs of burrow entrances. As the study progressed, individual animals were caught, marked and released (see Section 1.3) and their associated burrow entrance numbers noted. Any new burrows in the study area originating after the initial mapping of the first week were numbered and new measurements made.

In an aggregated population the density of individuals is high and space is limiting, and each individual will pre-empt an area (its territory) (Kaufmann 1983). This competition should manifest in the form of a lower limit to the distance between any calling male and its nearest neighbour. At high densities, the squared nearest neighbour distances ($r^2 = \omega$) are expected to be shorter than at low density. To detect regularity at high density, values of ω above a chosen value c are excluded from the analysis. The remaining data points below c is denoted N . \sqrt{c} is considered the greatest distance at which interaction occurs, although

sensitivity analysis has shown the value of c not to be critical to the results of this analysis (Pielou 1962).

The distribution of the truncated sample values ($0 < \omega < c$) is then compared with a similarly truncated distribution from a random population. The sample values (ω) are transformed with the probability integral transform to the variate y that has the property of being independent of the mean of the sample values (S). This y variate is then used to calculate the expected random distribution (Pielou 1962, 1977). First the chosen value of c is substituted, together with S into the equation

$$\frac{S}{c} = \frac{1}{c^\lambda} - \frac{e^{-c^\lambda}}{1 - e^{-c^\lambda}}$$

The Poisson parameter λ (denoting the mean number of individuals per circle of unit radius) is then solved by successive approximation. The sample values (ω) are transformed by

$$y = \frac{1 - e^{-\lambda\omega}}{1 - e^{-\lambda c}}$$

where y ranges from 0 to 1. A goodness-of-fit test is then used to compare the frequency of y with a rectangular distribution from a random sample. An absence of y values in the lower class intervals implies a regular distribution among calling males. The theoretical territory radius (ω_n) can be calculated from the sample of truncated nearest neighbour distances using c , S , and the variance of ω ($\text{var}(\omega)$). The equations

$$c - S = k \left(1 - \frac{1}{x} + \frac{e^{-x}}{1 - e^{-x}} \right)$$

and

$$\text{var}(\omega) = k^2 \left(\frac{1}{x^2} - \frac{e^{-x}}{1 - e^{-x}} \left[1 + \frac{e^{-x}}{1 - e^{-x}} \right] \right)$$

are solved for k and x . Since $\omega_h = c - k$, and $\lambda = x/k$, the Poisson parameter λ and the estimate of ω_h are obtained. A standard error of ω_h cannot be calculated, but an upper limit to ω_h is estimated by $\sqrt{(1/N\lambda^2)}$.

Because the gecko community is dynamic, with individual animals sometimes disappearing or moving between closely distanced burrow entrances, the mapping of calling sites of individuals investigated here was a 'snapshot' of the spatial patterning between individuals found within the same week that sound intensity readings were recorded from all the 15 vocalising males in the study population (see Section 2.2.1). In this way, the relationship between spatial patterning and sound intensity could later be investigated (see Section 2.3.2 below). Furthermore, for the analysis of competitive regularity, only nearest neighbour distances between calling males are required. For this reason, the nearest neighbour distances of an additional 13 vocalising males outside of the study area were incorporated in the analysis.

Bivariate kernel density estimators (Scott 1992) are used to plot the concentration of data points in three-dimensional space. The spatial arrangement of females and males over the study site are similarly investigated.

2.1.2 Results and discussion

The mapping of all active burrows in two-dimensional space on the study site is shown, together with vegetation and landscape features in Fig. 2.1. Twenty-eight nearest neighbour distances were obtained from each of 28 individual calling males. Nearest neighbour measures were not taken where topographical boundaries (i.e. small hills, low shrub) existed between nearby males as patterns of sound attenuation are affected by excess decay caused by such discontinuities. A histogram of squared nearest neighbour distances reveals that the sample population is aggregated (Fig. 2.2). The sample was truncated at a value \sqrt{c} of 15.5 meters, and all distances above this value were excluded from the analysis. The truncated distribution consisted of 20 nearest neighbour measures.

These 20 values ($S = 9.460$ m, standard deviation = 3.160) were transformed to the variate y , and statistically contrasted with a random distribution. The observed distribution of the transformed variate y is significantly different to that of an estimated random distribution, with no measures of y being present in the lowest class interval ($z = 1.825$, $P = 0.034$). The analysis of nearest neighbour distances clearly revealed a significant regular distribution of calling males at clumped densities. The distribution of y and the random distribution over 10 class intervals is represented in Fig 2.3. The estimated territorial radius was calculated to be 2.70 m, and the upper limit for this radius is predicted never to exceed 2.72 m.

The qualitative analyses of chorus patterning was useful in identifying trends in chorus organisation. Bivariate kernel density plots show clearly how gecko activity is concentrated around a focal locality - the centrally located patch of vegetation (Fig 2.4). A kernel plot of female density shows how females are congregated together on the immediate periphery of this vegetation and away from the bulk of calling males (Fig. 2.5).

2.2 Sound pressure

In investigating sound intensity as a mechanism in acoustic interactions, it is important to first look carefully at the way sound intensity attenuates away from calling males. The attenuation of call intensity with distance needs to be contrasted with that expected from the inverse-square law (Michelsen 1978). This physical principle states that if sound waves radiate spherically from their source, then the intensity (I_0) of such waves will decay at a rate proportional to the inverse of the square of the distance travelled from the source ($I_0 \propto 1/d^2$). Excess attenuation can be defined as that above which would be expected during optimal spherical spreading of a sound from its source according to the inverse-square law. Any disparity between the observed sound pressure decay and that expected from the inverse-square law implies that some ecological parameter(s) (e.g. vegetation) are introducing a source of excess attenuation (Marten & Marler 1977).

The vocalisation of *P. kochi* consists of a rapidly delivered number of 'clicks'.

Sonographic analysis (see Section 3.1) reveals that a typical call comprises a broad-band range of harmonics, between 0.8 and 4 KHz, with most energy present above 1.5 KHz (Fig. 2.6). Investigations in sound transmission show how at ground level, sounds below 1.5 KHz attenuate excessively (Marten & Marler 1977). However, at ground level low frequencies are still optimal for the maximisation of transmission distances providing that the frequencies are pitched above a range of attenuated low-pitched sounds, the limits of which vary to some extent with the habitat type. This range of least-attenuated frequencies corresponds to the envisaged sound 'window' of Morton (1975). In an open field, similar in topography to the inter-dune spaces, this window lies between 2 KHz and 4.5 KHz (Marten & Marler 1977). It appears therefore that an adaptive relationship may exist in the association between sound transmission and the physical properties of the call of *P. kochi*.

An interesting feature associated with vocalisation behaviour of *P. kochi* is that a male will withdraw his head into the funnel-shaped entrance of the burrow when vocalising. The entrance may function as a resonance chamber, amplifying the sound intensity of an emitted call. In fact, by calling upwards at an angle, the emitted sound is scattered over a wide area (Haacke 1969). This scattering may explain why humans find localising calling males by sound so difficult. Scattering may also offer some idea as to the patterning of the sound pressure field around a male's burrow.

The shape of the sound field produced by vocalising males will be important in mediating vocal spacing (Passmore 1981). If the pressure envelopes of *P. kochi* males are directional then individuals are expected to be spaced differently than they would if sound envelopes were spherical, owing to the different orientations of males with respect to one another. Sound intensity may be used as a proximate cue for judging nearest neighbour distance given any sound radiation pattern, although the most precise spacing would be evidenced in species with spherical sound fields (Telford 1985). The exact pattern of sound pressure attenuation of *P. kochi* calls was investigated.

2.2.1 Methods and materials

Sound pressure was measured with a Realistic Sound Level meter (fast setting) to the nearest 0.5 dB. Amplitudes were measured using the “A” weighting scale to reduce the masking effects of low-amplitude wind noise. This weighting should not interfere with the measurements of call amplitude as most energy in the gecko vocalisations occurs above 1000 Hz. All measurements of SPL were made 15 cm above ground level.

Geometric Averaging of SPL measures

Calculating an average SPL directly from a series of measures is complicated by the fact that the decibel scale is logarithmic. The arithmetic mean of SPL measures is in fact the geometric mean of the actual SPL values, and will always be less than, or in some cases equal to, the arithmetic mean of the sound pressures.

Cox (1966) formulated a lower bound for the error in not converting SPL to a linear scale. According to his formula, a range of 3.5 dB would translate into a calculation error of less than 0.18 dB. Because of both the relatively large magnitude of the sound pressure values and the logarithmic nature of the scale, error is negligible in the variation within individuals in this study (the maximum range is 3.5 dB within all 18 individuals). However, between-individual measures display appreciable variability (the range is 6.2 dB in the same sample of 18 animals) (see Section 2.2.2). Simple arithmetic averaging would not have sufficed here. In the calculation of average SPL values for individuals, SPL readings for each individual were converted to absolute pressure in μPa (0 dB SPL = 2×10^{-5} Pa), averaged and analysed. Where mean SPL scores are presented, these averages have been reconverted to decibels. Since standard errors (SE) are computed on the log scale, where confidence intervals are reported in decibels (e.g. in Section 2.5.1) these reconverted measures are asymmetrical about the mean.

Sound pressure radiation patterns

The shape of the sound field surrounding a caller was determined, in the horizontal plane, by recording SPL measurements (at 1 m) from directly in front of the subject (0 °), from one side (90 °) and from directly behind (180 °) (Fig. 2.7). Care was taken to ensure that the area around the subject was as uniform as possible. Five peak SPL

measures from 15 successive calls were noted from six individuals at all three angles. Ambient temperature was recorded with a Bailey instruments Model BAT-12 digital thermometer and was noted at each call. An ANCOVA is used to test for angular differences in sound intensity, together with individual differences while temperature is kept constant.

In order to gauge a more reliable measure of the levels of variability of between-individual vocalisation intensities, ten peak SPL measures from 15 successive calls were noted from an additional 12 individuals. Ambient temperature was also noted at each call. An ANCOVA is used to test for differences in sound intensity between individuals, while the covariance of SPL with temperature was again controlled.

Sound attenuation

The attenuation of call intensity with distance was measured every 10 cm from 50 cm to 140 cm (10 measures) from one individual (repeated measures - as with sound pressure radiation patterns above). These observations were compared with that expected from the inverse-square law. The degree of excess attenuation could then be gauged by the difference between the observed and the expected values.

2.2.2 Results and discussion

Patterns of sound attenuation of *P. kochi* closely followed the inverse-square law (Wilcoxon matched-pairs test: $z = -0.178$, $P = 0.859$; Spearman rank correlation, $r = 1.000$, $n = 10$). Patterns of excess attenuation are thus negligible. The pattern of observed intensity decay and that expected from the inverse-square law is depicted in Fig. 2.8.

SPL radiation patterns in *P. kochi* were found to be indistinguishable from that of a circular distribution (perfectly concentric around the intensity source) and independent of the effects of temperature (ANCOVA : temperature as covariate; $R^2 = 0.894$; Angle : $F = 0.587$, d.f. = 2,81, $P = 0.558$; Temperature : $F = 0.456$, d.f. = 1,81, $P = 0.502$). However,

individuals animals did display significant differences in their call intensities ($F = 107.008$, $d.f. = 5,81$, $P < 0.000$). When these data are pooled with those of an additional 12 individuals, individuals were still seen to differ significantly in intensity readings (ANCOVA : temperature as covariate; $R^2 = 0.885$; Individuals : $F = 89.926$, $d.f. = 13,165$, $P < 0.000$; Temperature : $F = 0.000$, $d.f. = 1,165$, $P = 0.502$). Sound intensity measures were seen to range minimally within individuals (maximum range within an individual = 3.5 dB, mean range = 1.18 dB) but quite extensively between individuals (range = 6.2 dB).

In several studies of anurans, the sound fields surrounding callers are not uniform (Licht 1976, Gerhardt 1975, Passmore 1981; c.f. Robertson 1984, Telford 1985). Conversely, the calling field surrounding vocalising *P. kochi* males was found to be perfectly uniform in all directions. The area and shape of a male's territory will depend on the density of surrounding vegetation and the distribution of nearby topographical discontinuities. In homogenous habitat, territory size was estimated from nearest neighbour analysis to be 2.70 m (Section 2.1.2). This corresponds to a sample SPL average of 62.4 dB (the mean SPL measure for males at 1 m was 71.3 dB). If all males in the population produced calls at the same intensity and had the same hearing sensitivity, then this value of 62.4 dB would represent the threshold value of sound intensity in the population (i.e. sound intensity is not expected to exceed this value 1 m from any resident calling male without invoking unusual or agonistic behaviour). However, there was considerable variation in the SPL measures of different males. A more dependable estimate of a threshold value may be derived by considering each pair of neighbouring males separately.

2.3 Modelling sound pressure decay

Since the propagation of intensity of the vocalisation of *P. kochi* obeys the inverse-square law, it makes sense to investigate the values at which neighbouring calling males intensities' overlap. If as other studies suggest, the patterning of males in the field is the result of some semi-invariant critical threshold of sound pressure not being exceeded (e.g. Robertson 1984,

Wilczynski & Brenowitz 1988, Brenowitz 1989, Telford 1985), then a relative constancy in SPL values should be observed between males that are well clumped.

Because SPL has been shown to vary significantly between individual males, a elementary derivation of a threshold value from the nearest neighbour analysis based on average SPL measures would be inadequate, as important information relating to between-male intensity variation will be ignored. Two alternatives exist for estimating a population threshold value : the first would involve conducting a semi-blind study using the nearest neighbour estimate as a mean for a range of selected intensities. These intensities could then be played back from a lower bound value of a selected range in SPLs and at increasing intensities to test males (e.g. Robertson 1984). While this approach would be necessary for the elucidation of an explicit threshold value, it cannot be considered a sufficiently rigorous experimental procedure alone, as any changes in behaviour observed over successive playbacks could possibly be due to repeated exposure to the test stimuli, or to the successive changes in signal amplitude (c.f. Brenowitz 1989).

A more realistic approach to obtaining an estimate of the SPL threshold value does exist. It is relatively easy to model the physical system of sound attenuation mathematically and to investigate a mapping (*sensu* Colgan 1978) between this system and the territorial gecko system under study. By looking at the decay in sound intensity radiating away from pairs of nearest neighbouring males a certain distance apart, the variation in SPL measures between males can be accounted for and a more reliable estimate of a threshold value may be obtained *a priori*. Once such a model is formalised, there are a range of important questions that are answerable. For example, morphological attributes and residency rankings (see method in Section 1.6) of individuals can be investigated to see whether they are in any way related to the magnitude of shared acoustic space between neighbours. Such a modelling appraisal would also be advantageous in generating a reliable set of intensity values that may be utilised in playback experiments (see Section 2.4.1 below).

2.3.1 The model construct

Let

$SPL(\text{gecko\#1}) = SPL(\text{gecko\#2})$ at some distance r'

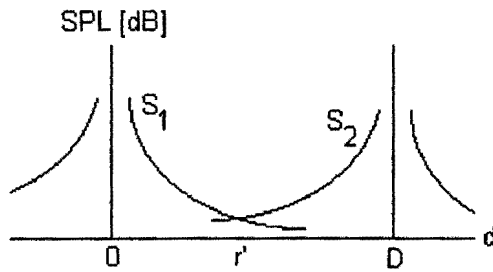
$SPL_1 = C_1 d^{-2}$ Let gecko#1 be at the origin, $d = 0$

$SPL_2 = C_2 (D - d)^{-2}$ where D is the distance from gecko#1 to gecko #2

$SPL_1 = SPL_2$ at distance r'

C = intensity at distance d ($dB = I_0$)

These curves are symmetrical about the sources - sound radiates in both positive and negative directions :



$$\begin{aligned} \frac{C_1}{d^2} &= \frac{C_2}{(D-d)^2} \\ \Leftrightarrow \frac{C_1}{C_2} &= \frac{d^2}{(D-d)^2} \\ \Leftrightarrow \frac{C_1}{C_2} &= \frac{d^2}{D^2 - 2Dd + d^2} \\ \Leftrightarrow \frac{C_1}{C_2} &= \frac{1}{(D^2/d^2) - (2D)/d + 1} \quad \text{provided that } d \neq 0 \\ \Leftrightarrow \frac{C_2}{C_1} &= (D^2/d^2) - (2D)/d + 1 \end{aligned}$$

$$\Leftrightarrow 0 = (D^2/d^2) - (2D)/d + 1 - \frac{C_2}{C_1}$$

$$\Leftrightarrow 0 = D^2 - 2Dd + \{1 - C_2/C_1\}d^2 \quad \text{Quadratic equation with two roots}$$

These roots are :

$$r' = \frac{2D \pm \sqrt{4D^2 - 4D^2(1 - C_2/C_1)}}{2(1 - C_2/C_1)}$$

$$\text{or } r' = D \times \frac{1 \pm \sqrt{(C_2/C_1)}}{1 - (C_2/C_1)} \quad (2.2)$$

hence the root lying $0 < d < D$ may be discarded. Units of C are irrelevant, as only the ratio of C_2/C_1 ($= I_{o2}/I_{o1}$) emerges as being important.

From (2.2), let $r_{x(n)}$ be

$$= n \sqrt{(D_1 \times \frac{1 - \sqrt{(C_1/C_x)}}{1 - (C_1/C_x)}) \times (D_2 \times \frac{1 - \sqrt{(C_2/C_x)}}{1 - (C_2/C_x)}) \times \dots \times (D_n \times \frac{1 - \sqrt{(C_n/C_x)}}{1 - (C_n/C_x)})}$$

i.e. the average (geometrically meaned) shared acoustic space of individual x surrounded by n neighbours

The patterning of r' in the sample population of 15 individuals can be investigated in several ways. The precision of r' (indexed by the coefficient of variation {standard deviation/mean}) with increasing nearest neighbour distance can be analysed for regularity at short lengths between individuals. Such regularity would imply the existence of a lower bound to the level of sound pressure between males. Second, a frequency histogram analysis will illustrate any skewing in the distribution of r' in the chorus population. Unequal intensities of callers could produce a range of frequency distributions, and the observed distribution of r' might be related to the degree of competition on the study site for calling territories.

The index $r_{x(n)}$ represents the shared acoustic space of any individual surrounded by n number of neighbours. Values of $r_{x(n)}$ where $n = 1, 2, 3$ and 4 for each of 15 individuals are investigated for any relationship with either morphological attributes or residency rankings. In this way it is possible to understand general correlates of acoustic territory size and

presumably resolve whether any neighbours, beyond the nearest neighbour, are important in territorial spacing mediated by SPL.

2.3.2 Results and discussion

The values of r' about the mean were seen more variable the further away that nearest neighbours were from each other. Values of r' became more precise at lower distances, and tapered off at even smaller distances (Fig. 2.9a). The distribution of r' shows a positive skewing, and this patterning is similar to that evidenced in the distribution of the squared nearest neighbour distances (Section 2.1.1) (Fig. 2.9b). Thus, there is evidence for regularity at small inter-male distances, and most neighbours shared relatively small acoustic territories, while a few individuals on the study site were more dispersed.

The averaged acoustic space ($r_{x(n)}$) showed no relationship to mass, length or extent of yellow colouration under any number of neighbours (Pearson product moment correlation : $r_{(\text{for all measures})} > -0.210 < 0$, $P_{(\text{for all measures})} < 0.477$). Lastly, $r_{x(n)}$ was investigated for any possible coupling with residency. A plot of residency status on $r_{x(1)}$ revealed a parabolic (\cap shaped) relationship (Fig 2.10). In order to assess the statistical validity of this relationship, $r_{x(1)}$ was truncated at its average value and residency scores above this value were transformed (where a previous ranking of 2 would now be a 4, and a 1 a 5 etc.). The strength of the relationship between $r_{x(1)}$ and the transformed residency scores was then analysed nonparametrically using Spearman rank correlation. The results displayed a significant tendency for more permanent individuals to have average-sized acoustic spaces, and for acoustic spacing to change with variation in residency status ($r = 0.881$) (Fig. 2.11). No such relationships were found between residency and $r_{x(n)}$ where $n \geq 2$.

While the model revealed a surprising absence of significant correlations of $r_{x(n)}$ with morphological features, $r_{x(1)}$ does bear an interesting relationship to residency - the shared acoustic space of an individual with its nearest neighbour was strongly dependent on its

residency status. Individuals with disproportionately larger and smaller spaces tended to be those that either disappeared fastest or reappeared only very occasionally. Individual geckos having average-sized acoustic spaces were those that were the most persistent chorus participants. This counter-intuitive finding is discussed further below (Section 2.5).

2.4 Playback Experiments

The role of vocalisations as a mechanism in inter-male spacing has long been known (Emlen 1968, Bunnell 1973, Whitney and Krebs 1975, Fellers 1979). SPLs have been measured for several species of anurans (Loftus-Hills & Littlejohn 1971, Gerhardt 1975, Fellers 1979, Passmore 1981), and the role of sound intensity in maintaining spacing between males has been investigated using playback techniques in several studies (Brenowitz *et al.* 1984, Robertson 1984, Telford 1985, Wilczynski & Brenowitz 1988, Gerhardt *et al.* 1989).

It is necessary to test whether, as the territorial analysis suggests, territorial males are indeed using the intensity of neighbouring calls to space themselves. Playback experiments provide a sensible approach for assessing whether SPL is used as the mechanism for such inter-individual spacing. Differential phonotactic responses of calling males to playback experiments, in which only intensity is varied, provides an approach that is both necessary and sufficient for this purpose.

Agonistic encounters between closely-venturing calling males have been observed (Section 1.5). Since male chorus spacing shows significant regularity at small nearest neighbour distances (Section 2.1.2), as does the patterning of variation of r' about the mean (Section 2.3.2), it is hypothesised *a priori* that there will be an upper threshold to the magnitude of sound pressure impinging on individual males, beyond which tolerance will break down between neighbouring callers. However, the gecko system is dynamic, with individuals moving about their numerous burrow entrances from evening to evening. Hence, given the once-off snapshot nature of the individual mapping sample (Section 2.1.1), it is expected that some-individuals will be spaced below this threshold, very few will be

exceeding this threshold, and most individuals ought to be sitting just below or at this threshold. This threshold model was explicitly tested using playback phonotaxis experiments.

2.4.1 Playback methodology

First, an *a priori* set of playback intensity values needed to be generated. Using SPL measures of 15 resident calling males in conjunction with nearest neighbour distances and the inverse-square law, the intensities (C) of neighbouring calls (i) impinging on their nearest neighbour (x) at 1 m (C_i1_x) were calculated in the following way :

Nearest neighbour distance (ix)	$C_i@x$	C_i1_x
D_{ix}	$C_i D_{ix}^{-2}$	$C_i D_{ix}^{-2} - 10 \log [(D_{ix} - 100)^2 / 1^2]$

Fifteen nearest neighbour distances and the corresponding intensity of these calls at 1 m from these individuals' nearest neighbours are used in generating intensity values for the playback experiments. The distribution of C_i1_x is shown in Fig. 2.12. This platykurtic (squat) patterning clearly reveals a constancy at which neighbouring call intensities overlap.

Playback values were selected at three intensities. First, the average intensity from a nearest neighbour impinging on an individual at 1 m was used as the estimate of where the threshold value in the population might lie. For this, the mean C_i1_x value from the sample was used (60 dB). For the other two playback values, upper and lower limits were first calculated by erecting 95 % confidence intervals on the spread of C_i1_x values. An upper limit was estimated at 62.8 dB and the lower limit at 54.9 dB (remembering that the SE is computed on a logarithmic scale and so these estimates will be asymmetrical about the mean once reconverted to dBs). The playback intensity level exceeding the hypothesised threshold value would lie above or at 62.8 dB and a value of 66 dB was selected. An intensity level falling significantly below the threshold value would lie at or below 54.9 dB. A value of 54 dB was chosen for this lower limit.

These selected playback values (54; 60; and 66 dB) are convenient as SPL drops by 6 dB with a corresponding doubling of distance from the source ($\Delta \text{dB} = 10 \text{ Log}(2^2/1^2) = 6 \text{ dB}$). This implies that SPL of the broadcast speaker can be calibrated accurately at one distance, and the desired SPLs obtained by accurately placing the speaker a certain distance away from the test subject in order to achieve these three desired playback intensities. In effect, owing to collinear dependency of SPL on distance, these differing playback intensities may be thought of as representing an actively vocalising male intruder (of average intensity) at different distances from the test subject.

The playback stimulus consisted of using the typically 'average' parameters of a sample of gecko calls in discriminant signal space (see Section 3.3) being played back at a constant rate (one call / 30 sec). A stimulus was broadcast to one test male at a time using one of the three intensities (making up one trial). The intensity of the playback apparatus was calibrated at 1 m and placed at one of three predetermined distances from a test male (0.5 m, 1 m or 2 m). The test male was given a five minute acclimation period (or less if he commenced vocal activity) before a trial began. Trials commenced when males were relaxed (active) and were only conducted on nights where the background intensity of wind fell well below the playback levels. Stimulus trials to test males were always conducted greater than 3 metres away from neighbouring males (see Section 2.1). Furthermore, trials within any one night were randomised over the study site so as to minimize the effects of pre-exposure of males in any one area. Calls were played back using the Marantz CP430 recorder and broadcast using a Blaupunkt HQS-300 pre-amplified speaker.

Responses to the playback trials (normal calling, antiphonal calling/vigilance, fight/flight) were noted after ten minutes. A normal calling response was scored when the test male continued with a normal (relatively low) frequency of calling, and did not display any unusual behaviour. Antiphonal calling or a vigilance response was scored when the test subject responded to the playback stimulus with an immediate call of his own, and continued to call at a greatly increased rate, interspersed with brief silent bouts where he would extend his body out of the burrow entrance and turn his head from side to side (as if 'listening'). Fight responses were scored when the test male 'charged' out of his burrow in the direction of the speaker - often stopping and waiting for the next call and then proceeding in the direction from which the stimulus originated. Flight responses were scored when, upon hearing the stimulus tape, the test male would rapidly retreat into his burrow and would not re-emerge for the duration of the trial. Non-responses were noted if

the test male failed to emerge from his burrow during the ten minute test period. The same trial was repeated three times on the same male on different nights before a non-response was scored.

Individual males were not tested more than once on any one night due to the potential danger of a carry-over effect influencing subsequent responses. It is reasonable to assume that the playback procedure is likely to stress the test subject. Any responses subsequent to the initial evening trial may well be dependent on the conditions of the first trial, and therefore cannot be considered an independent or a representative response. Trials were randomised over a sample ten individuals. Thirty trials were conducted (three trials at three intensities for each of ten individuals). Starting time of the trial and of the evening chorus, temperature, and the individual tested were all recorded at the beginning of any trial.

2.4.2 Results

The results of the playback experiments are presented in Table 2.1. Responses of males to the low intensity call (54 dB) showed a marked tendency to ignore the intruders (stimulus) call and to vocalise normally ($\chi^2 = 7.45$, d.f. = 2, $P = 0.015$, $P_{adj} = 0.045$). Responses of test individuals to calls of intermediate intensity (60 dB) showed a significant association with responding antiphonally/vigilantly ($\chi^2 = 10.5$, d.f. = 2, $P = 0.005$, $P_{adj} = 0.015$). Test males were inclined to charge the playback speaker or rapidly retreat into their burrow entrances when presented with the high intensity call (66 dB) ($\chi^2 = 10.5$, d.f. = 2, $P = 0.005$, $P_{adj} = 0.015$). Lastly, the null hypothesis that response type is independent of sound pressure over all three intensity categories was rejected (3x3 contingency table analysis: $\chi^2 = 29.182$, d.f. = 4, $P < 0.001$).

Individual males approaching the broadcast speaker in the loud (66 dB) trials with a charge response were not significantly heavier, louder or lengthier than those responding to similar trials with a flight response (Mann-whitney U : mass : $n_1 = 3$, $n_2 = 5$, $U = 9$, $P = 0.55$; SPL : $n_1 = 3$, $n_2 = 5$, $U = 9$, $P = 0.55$; length : $n_1 = 3$, $n_2 = 5$, $U = 11$, $P = 0.76$).

Interestingly, males having spent longer chorus site tenures (see Section 1.6) defending their burrows were more likely to charge the playback speaker ($n_1 = 3$, $n_2 = 5$, $U = 16$, $P < 0.03$).

The effects of the starting temperature and time of trial, evening starting time, mass, length, extent of yellow colouration and SPL of the test subject, trial sequence and the time elapsed from the start of the evening chorus were examined to see whether any of these may have had any affect on the documented phonotactic responses. None was found to have any significant influence (Kruskal-Wallis tests: starting temperature : $K = 1.455$, $n_1, n_2, n_3 = 10$, $P = 0.483$; starting time : $K = 4.933$, $n_1, n_2, n_3 = 10$, $P = 0.085$; evening starting time : $K = 1.997$, $n_1, n_2, n_3 = 10$, $P = 0.368$; mass : $K = 0$, $n_1, n_2, n_3 = 10$, $P = 1.000$; length : $K = 1.127$, $n_1, n_2, n_3 = 10$, $P = 0.569$; yellow : $K = 0.031$, $n_1, n_2, n_3 = 10$, $P = 0.984$; SPL : $K = 0.008$, $n_1, n_2, n_3 = 10$, $P = 0.996$; trial sequence : $K = 0.295$, $n_1, n_2, n_3 = 10$, $P = 0.863$; time from evening start : $K = 2.990$, $n_1, n_2, n_3 = 10$, $P = 0.224$).

2.4.3 Discussion

Several studies have reported active dissemination among anuran males whereby the amplitudes of neighbour's calls fall within a relatively narrow range or below some threshold value (Robertson 1984, Wilczynski & Brenowitz 1988, Brenowitz 1989, Telford 1985). The observation that the distribution of C_{i1x} revealed a relative constancy at which neighbouring call intensities overlapped lends direct support for the existence of such a threshold in *P. kochi*.

A threshold value above 60.0 dB was predicted based on the modelling of SPL between neighbour pairs. Interestingly, a threshold value of 62.4 dB was estimated using simply the theoretically estimated territory radius (Section 2.1.2) of male geckos and a measure of average SPL. Playback experiments exposed the degree to which the behavioural responses of males was dependent on the intensity of the playback stimulus. When a sound intensity of 60 dB was exceeded, aggressive or flight responses were elicited from resident calling males. Playback stimuli at this intensity of 60 dB evoked either antiphonal or vigilant

behaviour, and stimuli below this value resulted in no significantly different response to normal. These results are therefore consistent with the hypothesis that spacing in *P. kochi* is vocally-mediated and that sound intensity acts as the proximate cue through which individuals gauge the closeness of neighbouring males.

The experimental design of these playback experiments has persuasive internal validity (*sensu* Kroodsma 1989) with a completely randomised design being used to vary stimuli across the sample population of males. Order-effects (*sensu* Kamil 1988) are clearly controlled for.

One potential problem with using one stimulus to test for differential male responsiveness to variation in sound intensity is that this stimulus cannot be truly representative of all calls in the gecko population. There are several variable vocalisation features of males that may be informative during competitive interactions (see Section 3.2 'Call correlates'). These features have, by the nature of the single stimulus used in the experiment, been ignored. Studies have demonstrated that the call pitch (frequency) of anurans plays an important role in the assessment of fighting ability in aggressive interactions between anurans (Davies & Halliday 1978, Arak 1983, Ramer *et al.* 1983, Robertson 1986, Wagner 1989). Here, frequency is used by males to gauge the degree of fighting asymmetry before engaging in a contest.

There may be similar call features that act as important cues in *P. kochi*. Generalisations of the stereotyped responses to the utilised stimulus cannot really be made to other calls in the population, and the conclusion of this experiment therefore lacks a strong element of external validity (Kroodsma 1989). The extent to which vocalisation features are potentially informative, forms the basis of investigations in Section 3 (Vocalisations).

2.5 Competition conclusions

An investigation of competitive regularity using nearest neighbour analysis revealed evidence for significant territorial patterning in the inter-male spacing of *P. kochi*. Haacke (1974) stated that burrows of neighbouring males are rarely found closer than 2 m to each other. The finding here, based on an estimated upper limit to the territorial radius, that the burrow entrances of active males will never be expected to be closer than 2.72 m corroborates this statement. Males are thus aggregated on the study site, but maintain some critical minimum distance between themselves.

Geckos calling in a group may be able to advertise themselves more effectively and continuously than can a male on his own (Alexander 1975, Parker 1978). Collective chorusing may serve to attract gravid females from a larger area than an individual vocalising on its own, and may be beneficial for all males involved. However, once a female has reached the chorus it will be advantageous for each male to be individually distinct from his neighbours so that females may detect and select him as a mate. Telford (1985) documented female preferences for the most widely spaced call in *H. marmoratus*, and argued that such selective discrimination by females generates selection for males to maintain adequate inter-male spacing.

The amplitude of *P. kochi*'s call attenuated with distance in a predictable manner, and was also independent of the influence of temperature. The sound fields surrounding calling males were uniform. These characteristics imply that a precise mechanism of inter-male spacing, based on sound intensity, was possible. Furthermore, there was an impressive degree of constancy in the amplitude of neighbouring gecko calls at a focal male's position, despite a large degree of variation in inter-male distance. This finding is similar to that found in the neotropical frog *E. diastema* (Wilczynski & Brenowitz 1988). Also, males of *H. crucifer* were found to position themselves relative to each other such that the intensity of their nearest neighbours' vocalisation fell at a level that coincided with the peripheral auditory threshold for sound frequencies in the call (Brenowitz *et al.* 1984).

Both field measurements and experimental investigations have shown a role for neighbour call amplitude as the proximate cue regulating individual positioning in anuran choruses (Robertson 1984, Wilczynski & Brenowitz 1988, Brenowitz 1989, Gerhardt *et al.* 1989). Physical aggression amongst males maintains this level of spatial organisation by precluding conspecific intrusion onto the call site territories of residents (Robertson 1984, Telford 1985, Brenowitz 1989). Sound pressure was consequently investigated as a possible mechanism of inter-male spacing in the choruses of *P. kochi*, and playback experiments to males demonstrated that neighbours were unable to tolerate an intruder when the intensity of the intruder stimulus exceeded 60 dB. This study thus demonstrates directly the behavioural mechanism by which neighbour-call amplitude mediates inter-male spacing.

Behavioural models based on algebraic game theory (evolutionary stable strategy models) understand animal contests to be of two different kinds. Symmetrical contests occur when contestants are equally matched, and the contest is expected to be a war of attrition whose outcome will be dependent on the individual most willing to fight longer (Maynard Smith 1974). In contrast, asymmetrical contests will be dependent on the nature and the strength of the asymmetry (Maynard Smith & Parker 1976). Resource-holding power (RHP) asymmetries (Parker 1974) and payoff asymmetries (the differences in the consequences of losing or winning the contest for the two contestants) (Maynard Smith & Parker 1976) are two envisaged types of asymmetry.

Results of this section have revealed that prior residency is strongly coupled with both territory size (the most persistent males hold average-sized territories), and with the probability of a males behaving offensively in the face of a territorial intrusion. The observation that males having spent longer tenures defending their burrows are more likely to charge the playback speaker is intriguing.

Many studies have demonstrated that the prior owner of a resource is more likely to win in contests over that resource (Richert 1979, Davies 1978, Sigursj ndottir & Parker 1981, Haley 1994, Leuck 1995). This prior resident effect (Maynard Smith & Parker 1976) has been interpreted in many ways : First, prior ownership may be used as an conventional

uncorrelated asymmetry in contest resolution, and there may be no differences between prior owners and intruders (Maynard Smith 1974). Second, the defended resource may be more valuable to the resident than to an intruder, and prior residency corresponds to a payoff asymmetry (Leimar and Enquist 1984). Third, preceding residents may in fact be superior or stronger fighters than intruders (Leimar and Enquist 1984). Lastly, prior owners will be expected to possess more information about the worth of a resource and therefore be expected to fight for it. Intruders are likely to have little or no information about the resource and may not be prepared to fight so hard (Enquist and Leimar 1987). These hypotheses are non-exclusive. Grafen (1987) has argued that if the outcome of a contest is of critical importance, for example where mating opportunities are dependent on the outcome of very few fights, then asymmetries will be irrelevant to contest strategy.

Body size has most often been identified as the most useful cue in gauging RHP in animal conflicts (Parker 1974, Carpenter 1995). Size correlates with strength, and strength has been shown to an important factor in conflict outcome in many studies (Myrberg 1971, Jakobsson *et al.* 1979, Turner & Huntingford 1986, Clutton-Brock 1989, Beaugrand *et al.* 1996). However, size will not always be a reliable indicator of RHP because it will be influenced by differences in physiological or psychological condition (Clutton-Brock & Albon 1979, Robertson 1986). Most importantly, RHP will be affected by factors related to the history of the contestants, and several studies have documented prior dominance experience accounting for an increase in RHP (Francis 1983, Beacham & Newman 1987). While size contrasts between *P. kochi* opponents would seem the most likely determinant of dominance, there was no significant differences found between the morphological measures of males fleeing from and charging the playback speaker. This would suggest that residency (ownership) status contributes primarily to the determination of dyadic dominance between individual geckos fighting for a territorial space.

Understanding the biological significance of residency effects in *P. kochi* must involve some explanation relating to the costs of individual males acquiring and maintaining acoustic territories. This question is dealt with in more detail in Section 4 (Sexual selection), where the question of physiological costs to chorus participation are investigated, as well as the correlates of mating success.

Table 2.1 Results from playback experiments to males. Rows indicate stimulus intensities, and columns indicate response type. Bonferroni adjustments to the χ^2 probability levels are noted.

	Ignore/ Normal	Vigilance/ Antiphonal	Fight/ Flight	χ^2 statistic	Probability (P)	Adjusted Probability (P _{adj})
66 dB	0	2	8	10.5	**	*
60 dB	0	8	2	10.5	**	*
54 dB	7	3	0	7.45	*	*

* = Probability less or equal to 0.05

** = Probability less than 0.01

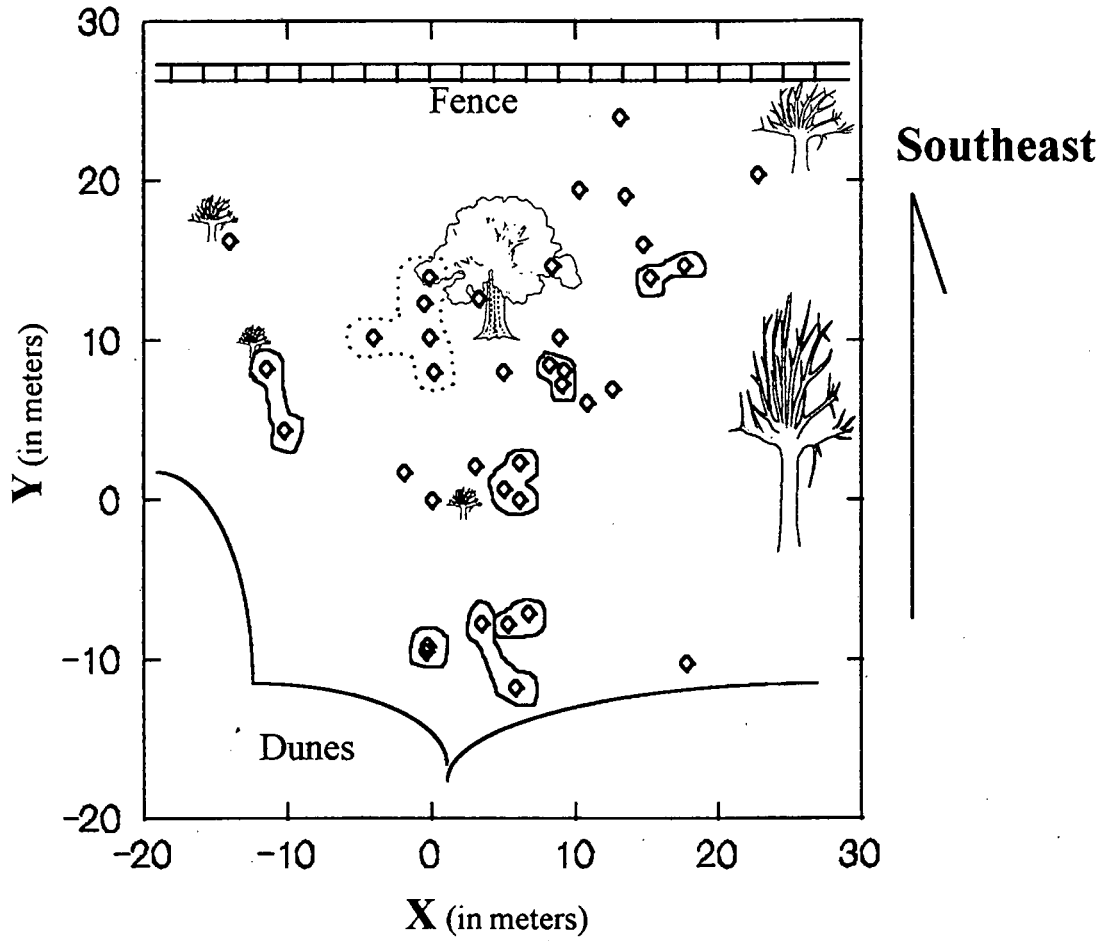


Fig. 2.1 A snapshot of active burrow entrances (♦) in two-dimensional space over the study site. The position of female residents is indicated by a dashed boundary. Where males were active at more than one burrow entrance, these burrow networks are indicated by an encircled solid line. Vegetation, topographical and landmark features are included.

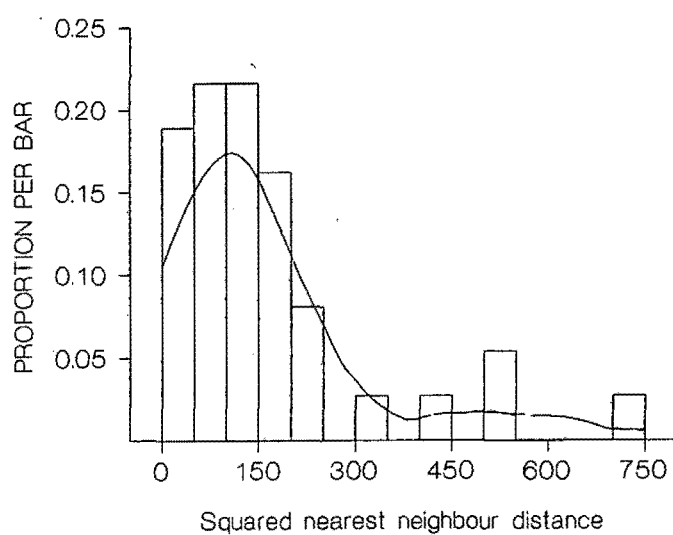


Fig. 2.2 A histogram of squared nearest neighbour distances of calling male *P. kochi*.

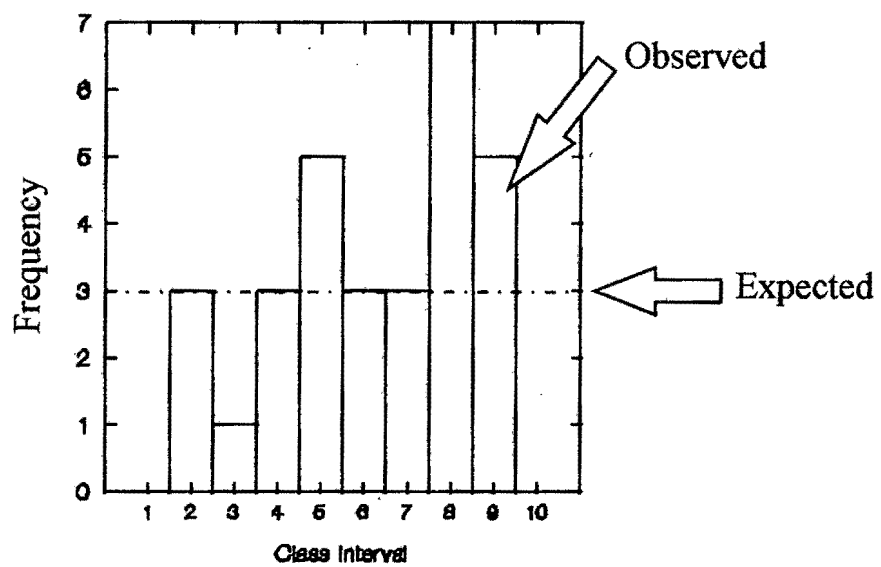


Fig. 2.3 The observed distribution of y (as indicated by the histogram bars) and the expected random distribution (illustrated as a horizontal dashed line indicating an expected frequency of 3) over 10 class intervals.

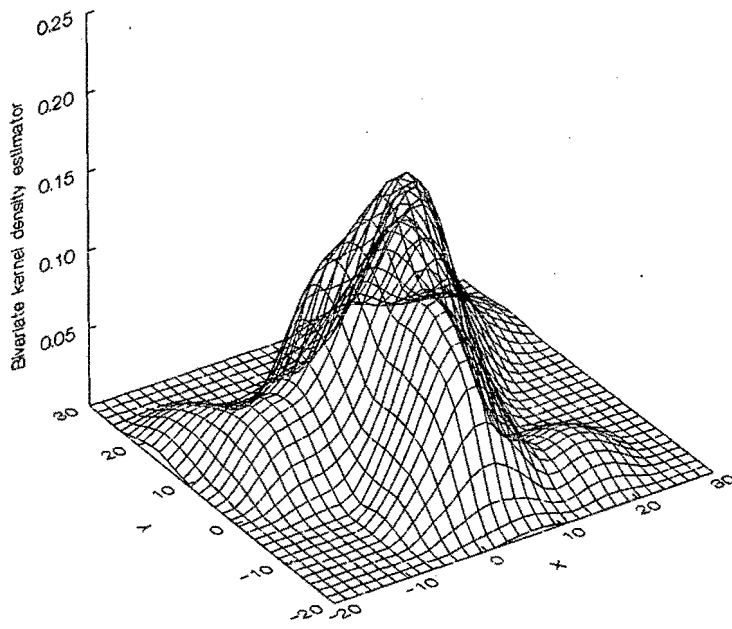


Fig. 2.4 A bivariate kernel plot representing the concentration of all gecko individuals in the study site population.

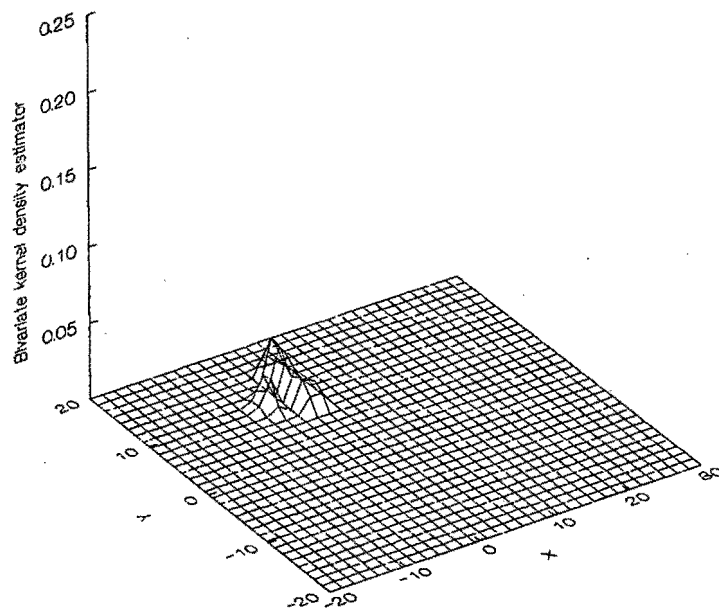


Fig. 2.5 A bivariate kernel plot representing the concentration of females in the study site population.

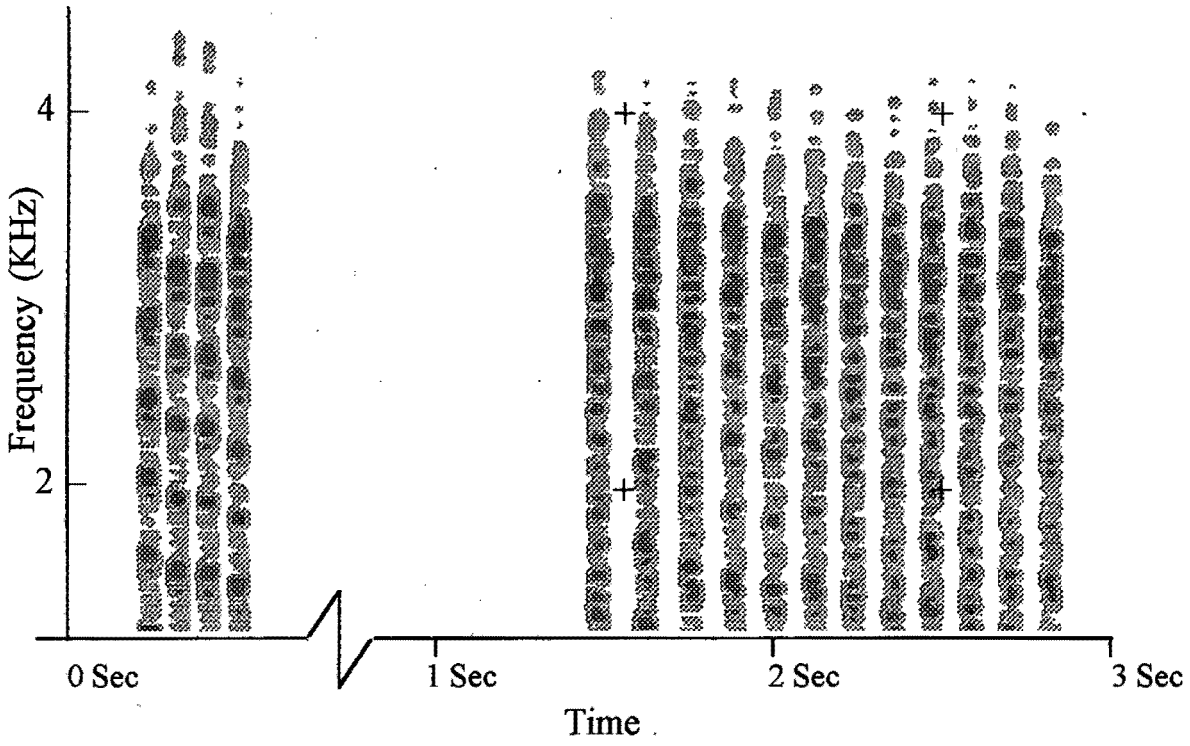


Fig. 2.6 A sonogram of the barking gecko's advertisement call. The tail end of one call is represented, followed by a complete call.

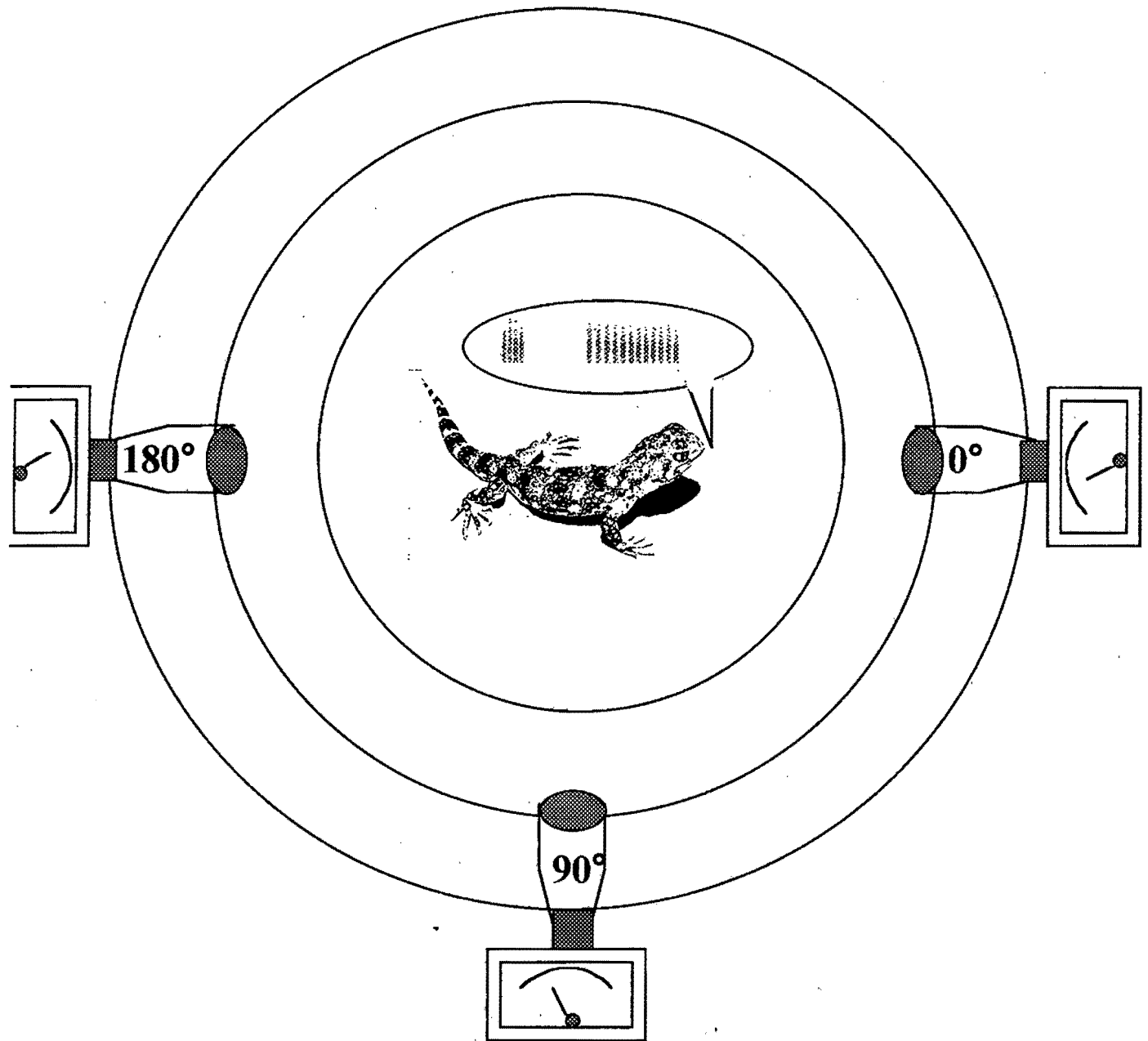


Fig. 2.7 The shape of the sound field surrounding individuals was determined by recording SPL measurements at 1 m from directly in front of a test subject (0 °), from one side (90 °) and from directly behind (180 °).

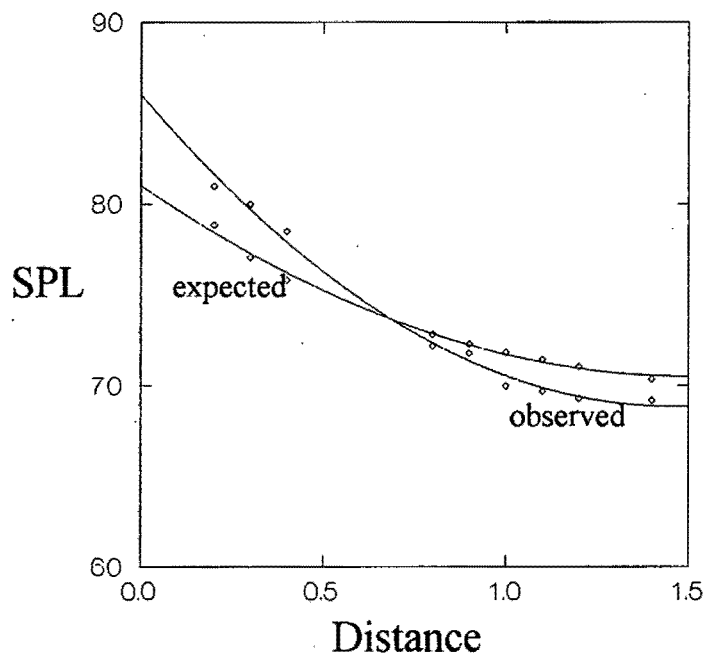


Fig. 2.8 Observed versus expected sound pressure attenuation with distance.

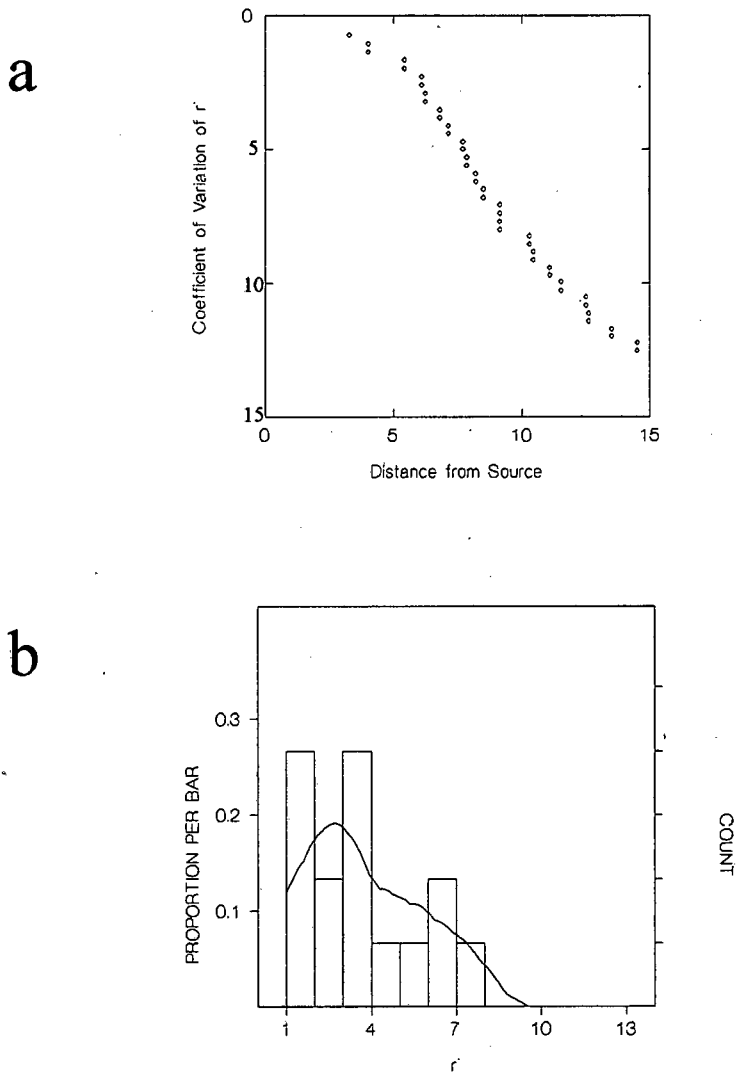


Fig. 2.9 Graphical representations of r' : (a) the variation of r' about the mean for nearest neighbour distances; (b) the frequency distribution of r' .

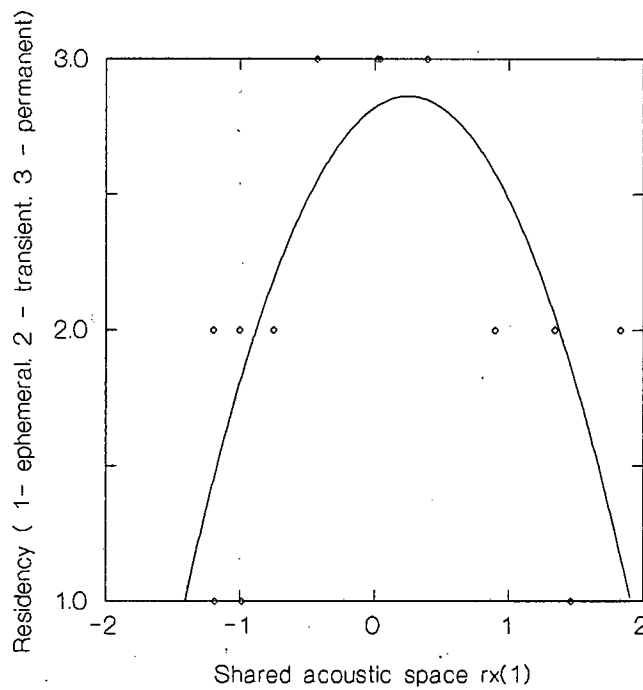


Fig. 2.10 A plot of residency and $r_{x(1)}$. The relationship reveals a parabolic trend. The sample size = 15, however, several data points overlay each other. Hence only 13 points are plotted here.

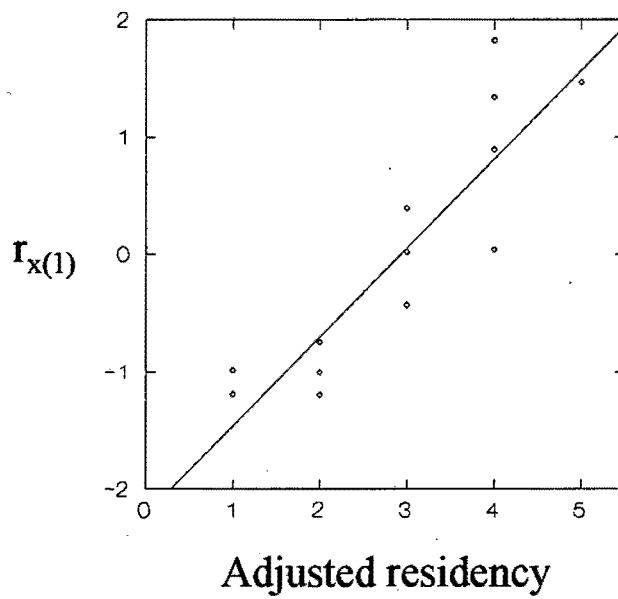


Fig. 2.11 The relationship between $r_{x(1)}$ and the adjusted residency scores. The strength of this relationship as indexed by Spearman rank correlation coefficient = 0.881. The sample size = 15, however, several data points overlay each other. Hence only 13 points are plotted here.

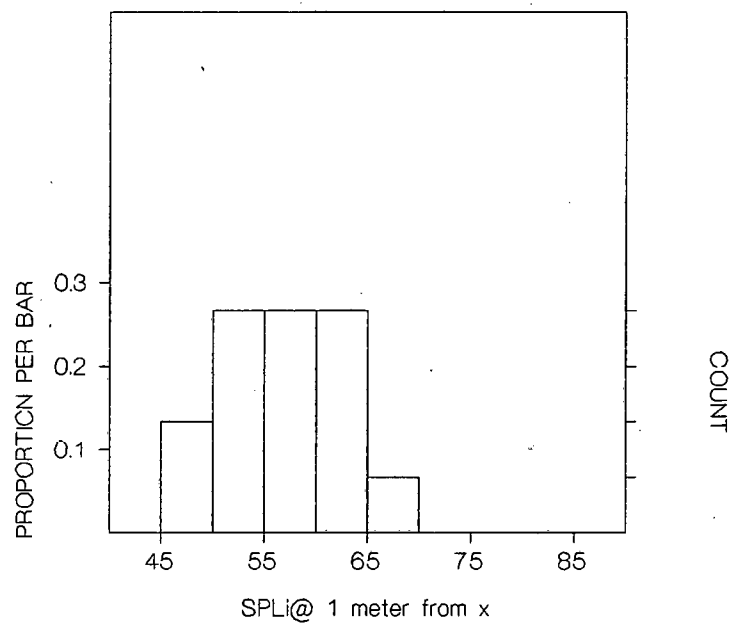


Fig. 2.12 The frequency distribution of $SPL_{(i)}$ at 1 m from individual x (C_{1x})

SECTION 3

Vocalisations

Our knowledge concerning the functional significance of gecko vocalisations appears to be restricted to males. The structures of male vocalisations are known from several species of geckos : *Cyrtodactylus kotschy* (Frankenberg 1978), *Hemidactylus frenatus* (Marcellini 1974) and *Ptyodactylus* spp. (Werner *et al.* 1978) and spectrograms of the vocalisations of *Gekko gekko*, *Hemidactylus turcicus* and *Phyllodactylus tuberculosis* have also been published (Marcellini 1977, Manley 1990). The functional significance of gecko vocalisations has long been debated : early anecdotal field commentaries suggest functions ranging from insect attraction (Beebe 1944) to ideas that calls were involved in aspects of social behaviour (Evans 1936, Brain 1962, Wever *et al.* 1963, Haacke 1969, Frankenberg 1974). Later studies have investigated the evolutionary significance of these vocalisations in a more rigorous way. Frankenberg (1982) showed how the male call of *H. turcicus* is produced by a dominant or territorial male towards other intruder individuals, and playback experiments to males of *H. frenatus* provided evidence that vocal displays function to establish and maintain territories (Marcellini 1977).

Interestingly, there appear to be impressive similarities in the call structure of several gecko species : the presence of a multiple-click call being well documented (Marcellini 1974, Haacke 1969, Frankenberg 1978, 1982, Werner *et al.* 1978). These multiple-click signals have a pronounced time structure which forms an optimal stimulus for the gecko inner ear (Manley

1990). Neurophysiological investigations in *G. gecko* have shown auditory-nerve fibres responding well to both spectral and temporal components (Manley 1990) and frequency sensitivity in other species (e.g. *H. turcicus*) has been noted (Sakaluk & Belwood 1984). It has been suggested, based on the basilar papillary structure of Gekkonidae, that hearing in these animals is expected to display convergent microphonic (sensory) properties (Wever 1978).

The call of *P. kochi* consists of a series of clicks uttered in quick succession, described most appropriately by Loveridge (1947) as “gack-gack-gack ...”. Haacke (1969) described the call as consisting of “...a series of clicks of apparently identical pitch and loudness..”. Haacke stated that the number of clicks per call varied from 9 to 16 with 11 to 12 clicks being the most frequent numbers sampled. Marshall & Cherry (1995) describe the call of *P. kochi* as starting loudly and then decreasing in volume. They also state that the number of “gacks” (clicks) per vocalisation varies between individuals, but is stable around a mean for individual males. However, none of these studies have made explicit use of robust sampling or control procedures (*sensu* Cochran 1977). Furthermore, few studies have made formal use of sonographic analysis techniques.

All signals convey information (Dawkins & Krebs 1978, Maynard Smith & Harper 1995), and the study of information theory (*sensu* Shannon & Weaver 1949) is the study of the uncertainty of transmitted information in a signal. The investigation of signal information is essential in order to cultivate an understanding and appreciation of the factors influencing the evolution of any communication system. However, investigations of signal information are often obscured by extraneous variability.

There are a wide range of studies where predictable covariation in body size with temporal and spectral characteristics of vocalisations have been documented (Marler & Hobbett 1975, Schubert 1976, Myrberg & Riggio 1985). For example, the calls of several anurans are influenced by differences in body size (Davies & Halliday 1978, Ryan 1980). It is also well understood that several elements of the behavioural repertoire of ectotherms are highly dependent on body temperature (reviewed in Willmer 1991) and the signal reception properties of many poikilothermic animals are also known to be influenced by temperature (reviewed in

Gerhardt & Mudry 1980). Similarly, the effect of temperature on the sensitivity of hearing in lizards is known to be profound (Werner 1976).

The influence of body size, age, or temperature can contribute substantially to masking the intrinsic differences or similarities between the vocalisation signals of different individuals. In a study of the information content of the song of the bushcricket (*Ephippiger ephippiger*), song structure was seen to change over the course of the breeding season. However, superimposed on this were consistent temperature effects. It was only when the influence of temperature was statistically controlled that individual males were seen to vary substantially in the way in which they showed ageing effects (Ritchie *et al.* 1995).

Perhaps then, one of the most intriguing aspects of the study of barking gecko biology lies in understanding the variation of their characteristic vocalisation. This section is aimed at answering a set of additional questions relevant to understanding the biological significance of the vocalisations of *P. kochi*. First, it is of interest to explore how the spectral and temporal features of individual's vocalisations correlate with intrinsic (morphological) and extrinsic (meteorological) variability. *A priori* ecophysiological considerations suggest that the calls of ectotherms should display an appreciable degree of plasticity that covaries reliably with both these sources of variability. Second, it is useful to understand more about the biological basis of the information contained in the acoustic variation between individuals, that is independent of intrinsic and extrinsic variation. The theoretical bases and the methodological intricacies of driving such a 'signature' analysis are discussed in detail, and a chosen statistical model is illustrated with a case study using vocalisations of both the eusocial naked mole-rat (*Heterocephalus glaber*) and *P. kochi*. Lastly, chorus activity is statistically modelled in an attempt to gauge the predictability of nightly chorus duration and to identify the primary factors that account for between-night variation in chorus duration.

3.1 General methods and materials

Individual geckos were caught, marked and released in the same way as outlined in Section 1.3 (Methods of marking, measurement and observation). Twenty calls were recorded from each of a total of 15 different males. Ambient temperature was noted at each vocalisation as temperature generally decreases throughout the night (see below). Two of the preliminary descriptor measure investigations made use of a smaller subset of this data set to ratify the presence of uncomplicated and anticipated features of vocalisation relationships (Sections 3.2.1 and 3.2.3). The total data set of 15 calling males (20 calls each) was used for other investigations.

Sound recordings were made with a Sennheiser ME66 super-cardioid capsule powered by a Sennheiser K6 module, and a Marantz CP430 recorder onto low noise TDK SAX cassettes. The ME66 capsule displays a flat frequency response that closely matches the frequency characteristics of the advertisement bark of *P. kochi*. All recordings were digitised onto a PC in 16 Bits and with a sampling rate of 22 KHz using Creative-Labs^(TM) soundblaster software (Soundblaster 1992). Fast fourier-transformations were performed using Spectrogram 2.3 freeware (Horne 1995). Frequency was measured to the nearest 12 Hz and duration to the nearest 1 ms using a screen-cursor.

The vocalisation of advertising males is characterised by a stereotyped series of rapid clicks. Prefatory sonagraphic analysis showed that each click consists of several harmonics regularly distributed between a lower (0.8 KHz) and an upper (4 KHz) frequency range (Fig. 3.1). Typically, two frequency bands dominate the frequency spectrum of any one call, one of these consisting of two to three harmonics, and the other simply one harmonic. There seems to be no stable association in the position of these two bands relative to each other : sometimes the broader band occurs below, and sometimes above the narrower band. These two emphasised bands display appreciable stereotypy within any one individual.

A total of 300 recordings were digitised into wavetable PC format, and decomposed into several descriptor measures (parameters) (see Fig. 3.1). These were : BCI (between-

call interval), DUR (duration of call), CLICK (total number of clicks in any one call), RANGE (frequency range of the broader emphasised harmonic) and AFREQ (average frequency of harmonic banding - see Section 3.2.2 below). This selection is initially arbitrary, and is based on the necessity to quantify those features that appeared from visual inspection of sonagrams to distinguish calls between individuals. In a random sample of 40 calls from 15 individuals, all measures proved significantly and highly repeatable (*sensu* Lessells & Boag 1987) (BCI: $r = 0.996$, $F = 3268.547$, d.f. = 39,40, $P < 0.000$; DUR, $r = 0.973$, $F = 37.067$, d.f. = 39,40, $P < 0.000$; CLICK, $r = 1.000$, $F = 3602 \times 10^{12}$, d.f. = 39,40, $P < 0.000$; RANGE, $r = 0.977$, $F = 44.154$, d.f. = 39,40, $P < 0.000$; AFREQ, $r = 0.976$, $F = 41.938$, d.f. = 39,40, $P < 0.000$). Summary statistics (e.g. mean, standard deviation) of all measures are presented in Appendix I.

Morphological measures (length, extent of gular yellow, and mass) were recorded as described in Section 1.3. Ambient temperature was measured on site with a Bailey Instruments Model BAT-12 digital thermometer. These measurements were standardised by placing the thermocouple 15 cm above ground level. Temperature was seen to decrease steadily throughout the evening from 18h00 (temperature = $-0.035(\text{hourly}) + 29.770$; $R^2 = 0.725$, $F = 90.618$, d.f. = 82, $P < 0.000$). Humidity was measured on site with a portable Vaisala digital hygrometer. The sound pressure levels (SPL) of calls of these males were also recorded. Sound pressure was measured with a Realistic Sound Level meter (fast setting). Amplitudes were measured using the "A" weighting scale to reduce the masking effects of low-amplitude wind noise. The logarithmic nature of the decibel scale and SPL averaging is dealt with in these analyses as in Section 2.2.1.

3.2 Call correlates

In this section, the relationships between call descriptor measures are investigated in an effort to eliminate latently redundant descriptors, and to maximise the information contained in utilised descriptors. Emphasis is placed on examining the covariance of temporal characteristics (duration and call rate) of *P. kochi* vocalisations with temperature and over

time. The frequency distribution of click number of the calls of *P. kochi* is similarly examined. Lastly, the existence of linear relationships between call descriptor measures, and morphological and temperature measures are explored.

3.2.1 How informative is between-click interval?

As a preliminary step in the choice of useful call descriptor measures, the temporal measure of between-click interval (the time-lapse between the end of one click and the beginning of the next click) (Fig. 3.1) was studied in an attempt to understand its predictability. The vocalisation of the barking gecko is made up of a series of clicks, and the intervals between each click are not equal, but decay in a hyperbolic fashion (starting off relatively long and then shortening towards the end of the call). The hypothesis, that the patterning of between-click intervals within and between individuals represents no more than an invariant function of duration and click number within the population, was examined. An acceptance of this idea would greatly simplify subsequent analyses as between-click interval could then be considered redundant, and excluded from further investigation.

An investigation using a sample of 20 calls from one individual revealed a high degree of collinearity between call duration and click number (Pearson product moment correlation : $r = 0.878$). The measure of average between-click interval (the sum total of between-click intervals divided by the total number of clicks in any call minus one) was seen to be strongly dependent on the total number of clicks in any call ($r_{\text{(for all of 20 calls)}} > 0.920$). This suggests the relationship between call duration and click number is strongly interdependent, and that a composite index of duration and click number might display little more information (in terms of inter-individual variance) than either measure presents on its own.

Using the same sample of 20 calls from one individual, average between-click interval was seen to be strongly related to the composite index of duration/click (DOC) ($R^2 = 0.931$, $F = 326.193$, $d.f. = 1, 18$, $P < 0.000$). The relationship between average between-click interval and DOC was estimated from a least-squares regression analysis to be :

$$\text{average between-click interval} = 0.781(\text{DOC}) + 3.986 \quad (1)$$

The residuals of this linear model fit are apparently homoscedastic. It is important to test whether the simple relationship evidenced in equation (1) from an examination of between-click interval from one individual is invariant among the population at large. For this purpose, an additional five individuals were incorporated in the analysis, each individual comprising of a sample of 20 calls. First, observed average between-click interval was calculated for each of 20 calls for each of these five individuals. Second, expected average between-click intervals were generated by substituting the values of DOC for each call into equation (1) above. Each individual's observed scores for between-click interval was regressed on the expected scores, and together with the first individual, the residuals were stored. Residual patterns were analysed using a one-way ANOVA. The results show no significant difference in the residual scores between these six individuals ($F = 0.598$, d.f. = 5,114, $P = 1.000$). The relationship between average between-click interval and DOC implicit in equation (1) is clearly invariant in the sample population (Binomial exact : 6:0, $P = 0.016$). Hence, it is prudent and also convenient to exclude between-click interval as a descriptor measure in any further analyses.

3.2.2 Peak frequency or averaged harmonic structure?

Another profitable question to ask at the onset of this section is how to sufficiently encapsulate the variance associated with harmonic banding of the vocalisations. As mentioned above, the call of *P. kochi* displays several harmonics distributed regularly between the lower and upper frequency ranges. These harmonics are closely packed, giving the call a broad-banded appearance. However two frequency bands dominate the frequency spectrum of any one call, one consisting of a wider band of two to three emphasised (louder) harmonics, and the other simply one emphasised harmonic (Fig. 3.1). It is of interest in attempting to establish the most useful frequency descriptor measure to look more carefully at the variance of this band patterning. Ideally, the variance present in the two emphasised frequency bands can be summarised suitably in a predictive index.

Examination of 20 calls from each of a set of seven individuals shows how the middle frequency of the wide-band predictably covaries with the mid-frequency of the narrower band (sample covariance = 836938.7). A composite index (simply the average of the two frequencies) results in a convincing predictor of the variance of either band ($R^2 = 0.995$, d.f. = 1,138, $P < 0.000$). This measure, average frequency (AFREQ), is thus used as the frequency band descriptor measure.

3.2.3 How do call duration and rate decrease over time?

Temperature in the inter-dune spaces decreases throughout the night, as does call rate and call duration (as witnessed by the steady increase in between-call interval and call duration of any one individual's vocalisation over an evening). It is of interest to know how independent this slowing of duration and call rate is of temperature, and also whether different individuals' call rates and call durations decay at different rates.

First, call duration was examined. Using the sample of 20 calls from each of 15 individuals, duration was regressed on temperature ($R^2 = 0.694$, d.f. = 14,285, $P = 0.001$). Duration is consistently inversely related to temperature (the correlation coefficient, r , is negative). The residuals from the regression analysis were stored in standardised form (normal deviates : mean = 0; variance = 1) as absolute values of duration are not of interest here, but the way in which duration changes throughout the evening is. These residuals effectively represent scores where the covariance of duration with temperature has been removed. The standardised residuals are then entered as the dependent variable in a two-way ANOVA. Call number (the coding for the sequence of calls an individual emitted on an evening), and time difference (the elapsed time between the start of the evening chorus and the start of the recording) were entered, together with their interaction, as factors in this model. The output shows that while the model is significant ($F = 3.416$, d.f. = 3,296, $P = 0.05$), the percentage variance accounted for is minimal ($R^2_{\text{adj}} = 0.015$). The only factor that comes out as being statistically significant is time difference. When time difference is

entered as the sole factor in the ANOVA model, the results do not change substantially ($R^2_{\text{adj}} = 0.018$, $F = 6.340$, $\text{d.f.} = 1,298$, $P = 0.012$).

It is expected that time difference will account for a certain percentage of the variance of the standardised residuals of duration on temperature. However, this variance is seen as trivial. Clearly, duration does not decline significantly over the evening, anymore than could be predicted by change in temperature. It is also expected that since call duration is so markedly dependent on temperature, it would be unlikely that significant differences exist in call duration between individuals. The same standardised residuals of call duration on temperature were analysed as a one-way ANOVA, with individual levels being entered as the only factor. Individuals are seen not to differ in call duration ($F = 1.157$, $\text{d.f.} = 3,296$, $P = 0.283$).

Second, the hypothesis that individuals do not differ in their call rates independently of the influence of temperature was tested. BCI was first transformed to normality using a log-transformation. Using the sample of 15 individuals and 20 calls each, logBCI was regressed on temperature. It was seen that logBCI did not display a marked dependence on temperature ($R^2 = 0.102$, $\text{d.f.} = 1,298$, $P < 0.000$). The residuals from each regression were stored in standardised form. Again, the standardised residuals were then entered as the dependent variable in a two-way ANOVA with call number, time difference and their interaction as factors. The results show that these factors fail to account for any substantial portion of the variance of the standardised residuals ($R^2_{\text{adj}} = 0.001$, $F = 0.501$, $\text{d.f.} = 3,296$, $P = 0.682$).

An ANCOVA (comparison among multiple slopes) was performed to gauge whether different individuals' BCIs slowed down at different rates. The unstandardised logBCI scores were treated as the dependent variable, with individual levels acting as the factor and temperature as the covariate in this analysis. The results show clearly that individuals' BCI's decay at significantly different rates, and that this is independent of the effects of temperature ($R^2_{\text{adj}} = 0.819$; $F_{\text{temp}} = 2.743$, $\text{d.f.} = 1,270$, $P = 0.100$; $F_{\text{levels}} = 37.534$, $\text{d.f.} = 14, 270$, $P < 0.000$). The interaction between individual levels and temperature was not

significant ($F = 1.237$, d.f. = 14,270, $P = 0.500$). Thus, individuals were not sampled under different temperature conditions.

3.2.4 Whither click number?

As mentioned in Section 1.1, much of the past emphasis on distinguishing between the various species of *Ptenopus* has been placed on the documented differences in the number of clicks present in each species' vocalisation (Haacke 1969). These past analyses have been very thorough in generating a reliable, yet small sample of tape recordings that demonstrate quite convincingly the nature of the spread in number of clicks per call of *P. kochi* (Haacke 1969, 1975). The set of sample recordings collected for this current research project represents the largest sample to date ($n = 300$) of where click number has been rigorously quantified.

Frequency analysis of click number shows that while the average click number for *P. kochi* is 12 - as reported - the range of the observed number of clicks per call (6-18) extends beyond that reported (9-16). These data are summarised in Fig. 3.2. It is interesting to note that the present study reveals no relationship between click number and temperature (Pearson's $r = 0.000$). Thus, information regarding click number need not be accompanied by temperature information for it to be useful in interspecific comparisons. Temperature during the recording sampling period varied moderately (mean = 22.6 °C, standard deviation = 3.2 °C, range = 13.3 °C, minimum = 15.4 °C, maximum = 28.7 °C).

3.2.5 General call correlates

Lastly, the remaining relationships between call descriptor measures, and morphological and temperature measures were investigated using the complete data set ($n = 300$ calls). Only statistically significant relationships are presented here. LogBCI was seen to be inversely related to both mass and temperature (Pearson r : mass : $r = -0.410$; temperature : $r = -$

0.320). Heavier males call more often than lighter ones, and individuals call less frequently at lower temperatures. DOC is positively related to both mass and to length, but inversely with temperature (mass : $r = 0.240$; length : $r = 0.240$; temperature : $r = -0.681$). Hence, heavier and lengthier individuals are the ones most likely to produce the longer calls, and call length is strongly related to ambient temperature. RANGE is related to mass ($r = 0.476$). No significant correlates of AFREQ was found.

It is important to note that while all the above relationships are statistically significant, the strength of most of these relationships (as indexed by the magnitude of the correlation coefficient - r) are surprisingly weak. Also, no significant correlates of some descriptors are detected (e.g. AFREQ). This might be due to their being an authentic absence of observable linear relationships between call descriptors, and morphological and temperature measures. Alternatively, it could be possible that more effective predictors of vocalisation features may be found in linear mathematical composites of morphological and meteorological measures. For example, call rate may not be simply related to mass, but may be better understood by a combination of morphological features, say mass divided by length.

The process of finding more appropriate linear indexes requires computer intensive statistical modelling, a process undertaken in the ensuing section. Furthermore, an understanding of the unexplained (residual) variance associated with call descriptor measures is best approached through a comprehension of information theory (*sensu* Shannon & Weaver 1949, Moles 1963). The next section introduces the conceptual framework of information theory, and demonstrates how such an approach can best be used to understand the potential functional significance of the vocalisation of the barking gecko.

3.3 Information content of vocalisations : summary

Individual recognition is a central concept of interest to behavioural research - researchers desire to understand the importance of signalling individuality in cooperative and competitive contexts. Among the more obvious testing grounds has been the analysis and manipulation (playback) of vocal signals, and an immense number of such studies have appeared in the literature. The currently accepted operational definition of a 'signature' refers to a specific complex of phenotypic traits which is (to some degree), individually distinctive. According to this definition, selection for individual recognition can produce a signalling system where individuality will be encoded in a specific complex of phenotypic characters (signal space). However, considerations in information theory suggest that in signalling systems where individual distinctiveness is of functional significance, there should be no predictable degree of blending or patterning in signal space. It follows that rigorous evidence of individuality in signal space is required to infer that individual distinctiveness has been selected for. Analytical and experimental research into the functional significance of vocalisations requires the establishment of the existence and extent of covariation in call structure with obvious morphological and extraneous factors (e.g. mass, temperature). Statistical examination of this covariation must be sufficiently refined to incorporate controls that can distinguish between individual- and extraneous-based variation discrimination. This approach is essential before a signature function may be invoked.

Using a novel analytical method that aims to control for predictable patterning in multidimensional signal space, a covariate-adjusted approach to discriminant-function analysis (DFA) was found most appropriate for these investigations (Rao 1966). The soft-chirp vocalisation of *H. glaber* and the advertisement bark of *P. kochi* were analysed in a case study designed to test the inherent feasibility of covariate-adjusted multivariate techniques in the study of inter-individual acoustic variability.

3.3.1 Introduction to signature systems

The evolutionary significance of individual recognition gained prominence with the birth of modern sociobiology (Wilson 1975). Prior to this, ethology was rapidly becoming a quantitative science with some of the early work focusing on individual recognition particularly in colonial-nesting seabirds (Beer 1969, Stevenson *et al.* 1970). By the late 1970's numerous studies had attempted to analyse and compare individual vocalisations (Table 3.1) or had provided experimental evidence for the role of these signals in individual recognition (Table 3.2). This early body of empirical work has been ably reviewed by Falls (1982).

More recent work on individual recognition has followed a similar route viz., experimental verification of an individual recognition function for a signal using call playback techniques, and identifying, in a statistical sense, the parameters of a signal which potentially encode individuality. Halpin (1991) correctly pointed out that less is known about the actual cues used for individual recognition than is known about their recognition function. She stressed the need to address this imbalance because, “an understanding of the ‘identification’ component and of the cues used for identification is essential if we are to develop a complete understanding of the mechanisms of kin recognition” (Halpin 1991, p. 222). Similar sentiments underpin most theoretical considerations of the evolution of signature systems (e.g. Beecher 1982, Beecher *et al.* 1985, Beecher 1989).

Beecher (1982, p. 478) introduced the idea of a 'signature' system as a mechanism of identification. Here, a signature refers to a “specific complex of phenotypic traits which is (to some degree), individually distinctive”. According to this definition, selection for individual recognition can produce a signalling system where individuality will be encoded in a specific complex of phenotypic characters (hereafter termed ‘signal space’). Beecher’s novel approach, which is an extension of the fundamental principles of information theory (Shannon & Weaver 1949, see Pierce 1961, Moles 1963), has contributed considerable understanding to the potential for such signature systems, and the conditions for their functioning (Beecher 1982, Beecher *et al.* 1985, Beecher 1989). This work has provided a necessary focus for the investigation of the information capacity of signals, as well as a basis for comparative analyses between species. The

significance of these contributions is acknowledged, but it is considered that the evidence needed for invoking individual recognition requires further elaboration

For example, less accurate signal systems that do not precisely encode individual distinctiveness are often described as signatures but only because they fall within the scope of the currently-accepted operational definition (see above). These less exacting signal systems may have arisen from fortuitous correlations with phenotypic traits or with extraneous variability, and may consequently not be functioning (*sensu* Williams 1966) in individual recognition per se. Discrimination in these instances may be based on morphology, sex or even ambient sampling conditions. Essentially, the resultant pattern of proactive discrimination may be one that is superficially indistinguishable from individual recognition. It is suggested that a definition not based on the adaptive significance of individual recognition is insufficient to invoke a signature mechanism. It is therefore proposed that Beecher's (1982) definition is too loose in identifying signature systems as 'to some degree' individually distinctive.

Information theory is the study of the reduction in the uncertainty of a signal (Shannon & Weaver 1949). This theory predicts that in signalling systems where individual distinctiveness is of functional significance, there should be no predictable degree of blending or patterning in signal space (see below). It therefore follows that evidence of individuality in signal space is required to infer that individual distinctiveness has been selected for. Where individual recognition may be an effect (*sensu* Williams 1966) of more complex cognitive processes, a signature system cannot be advocated without first subjecting this explanation to a suitable test.

A methodology for quantifying individuality in such a rigorous way has not been precisely formalised. The methods proposed here may be unworkable when dealing with animals possessing known multiple signalling traits (the statistical 'teasing' out of individually distinctive signals from phenotypic noise becomes intractable), but 'signature' predictions are testable in simpler systems where the signal is discrete and limited to one sensory modality (e.g. sound). Establishing the true prevalence of signature systems is of tremendous heuristic worth especially when distinguishing between selection for the evolution of signature systems, and other forms of adaptive communication between conspecifics (i.e. size or class discrimination). It is argued that

to date, the statistical and experimental approaches to testing for individual recognition cannot make this distinction.

3.3.2 The search for individual recognition cues

Several levels of investigation into individual recognition cues have been adopted, and the level of sophistication has advanced with time (see Table 3.1). The first type of approach was simply a qualitative visual inspection of sonagrams or spectrograms (e.g. Munding 1970, Brooke 1978). Several early studies also made use of the coefficient of variation to describe precision of call measures within individuals (Hutchinson *et al.* 1968, Waser 1977). More complex univariate statistical procedures were also introduced to test variability within and between call measurements (Miller 1978, Sieber 1985). Currently, a multivariate level of analysis is considered the most suitable approach to understanding the basis of individual recognition cues (Gelfand & McCracken 1986, Jones *et al.* 1987, Jones *et al.* 1991, Bauer & Nagl 1992, Chaiken 1992, Scherrer & Wilkinson 1993, Hammerschmidt & Todt 1995, Lessells *et al.* 1995, Robisson *et al.* 1993, Masters *et al.* 1995, Obrist 1995). Beecher's information theory approach has already been mentioned (Beecher 1982, 1989).

However, there seems to be no strict consensus over what constitutes the appropriate statistical approach for establishing the basis of a vocal signature. The root of this problem lies in how to establish the existence of unique characteristics within a signal. Beecher (1982) views an individual signature system as a pattern system in which several independent dimensions provide the basis for discrimination. However, regardless of the level of analysis, any size, sex or meteorologically based covariation with signal structure has consistently been overlooked as a possible source of masking of individual distinctiveness. As is argued here, this has obvious biological relevance.

One early attempt at a fairly sophisticated analysis of individual signal variation was that of Symmes *et al.* (1979). Here the individuality and stability of isolation peeps in squirrel monkeys (*Saimiri sciureus*) was investigated using multivariate analysis procedures. This

study revealed that individually distinct combinations of acoustic features characterise the isolation peep and that such combinations persist over several years, but also that the mathematical representation of an individuals' peep structure were not all equally separated. The authors state that mathematical treatment of clusters cannot clarify the issue of relative acoustic individuality or permit conclusions as to the number of individuals that might be recognized by call alone in a troop. The authors nevertheless conclude that the vocal identity of an individual is encoded in the isolation peep. The signal has structural consistency within individuals that persists over time, and is thus defined as a vocal 'signature' (Symmes *et al.* 1979).

Multivariate analyses of the functional significance of acoustic behaviour are common. Steiner (1981) investigated species differences in the whistle vocalisations of five north Atlantic dolphin species using DFA to compare overall whistle structures within and between species. The Mahalanobis D^2 statistic was used as the measure of the differences between overall whistle forms as determined by the distance between mean vectors in multivariate space. The degree of differences in whistle vocalisations among the five species correlated with the taxonomic relations of the five species. Goldstein (1978) has used 12 characteristics measured from sonagrams in a uni- and multivariate statistical analysis into the dialects of female Bobwhite (*Calinus virginianus*) "Hoy" calls. Similar approaches exist for the analysis of vocal repertoires (e.g. adult pikas - Conner 1985a). The understanding that sex-based covariation is an important consideration in vocal studies is also present in the literature (e.g. Marler & Hobbet 1975, Taoka *et al.* 1989, Sayigh *et al.* 1995). Lessells *et al.* (1995) analysed the individuality and sexual differences in the provisioning calls of European bee-eaters (*Merops apiaster*), and concluded that individual differences exist, but sex differences are relatively minor. An interesting study in anuran morphometrics utilised among other things, principal component analysis to look at the possible artifacts introduced by specimen preservation (Lee 1982). Ordination of the first two principal components reveal associated factor loadings with nearly all variables loaded heavily on principal component one. The first component, which accounted for 70.5% of the variation in the data, was interpreted as a size-based factor.

3.3.3 Identifying a signature

The critical feature of an identification (signature) system in social groupings is its potential to facilitate individual distinctiveness (i.e. the signature must 'pack' a lot of information). In order to get individual distinctiveness on a reasonable scale, a pattern system in which several independent dimensions encode individual uniqueness is likely, rather than a single graded variable (Beecher 1982).

Information theory predicts that a considerable degree of overlap between individuals is unlikely in an effective signature system (Beecher 1982). Selection for a functional 'signature' should manifest as a patterning in signal space in which individual distinctiveness is encoded. This pattern should be evident even when looking at all the animals in a social group. Beecher (1982) also makes the point that if a signature system has evolved for that purpose, then one expects the number of potential signatures to exceed the upper limits of the natural population size to reduce the probability that any two individuals have the same signature. However, closer inspection of Beecher's (1982) definition of a signature reveals a relevant oversight. In defining a signature as a "specific complex of phenotypic traits which is (*to some degree*), individually distinctive" the importance of the overlap between the signal space of individuals will be ignored (*italics mine*).

This problem is most apparent in the sound communication literature where the accepted analytical approach is to first decompose the characteristics of a sample of recorded calls into a number of descriptor measures (duration, frequency range etc.). Multivariate statistical procedures (most often DFA, see Table 3.1) can then be used to see whether the identity of the caller is encoded in hyperspace. If any nonrandom pattern of individual grouping is evident, this is used as evidence of a 'vocal signature' (Hafner *et al.* 1979, Symmes *et al.* 1979, McArthur 1982, Gelfand & McCracken 1986, Jones *et al.* 1987, Esser & Schmidt 1989, Gouzoules & Gouzoules 1990, Tooze *et al.* 1990, Weary *et al.* 1990, Obrist 1995, Sayigh *et al.* 1995). The relevance of overlap or predictable patterning in spectral measures has largely been ignored. For example, Gelfand & McCracken (1986) note that several call parameters of Mexican free-tailed bat pups (*Tadarida brasiliensis*)

significantly covary with age. Moreover, the majority of the variation ($> 69\%$) in four out of nine call descriptor measures could be significantly predicted by considering pup age. Nevertheless, the authors conclude that the pups have individual vocal signatures. The 'signature' vocalisations of timber wolves (*Canis lupis*) were investigated in a similar way (Tooze *et al.* 1990). Both principal component and DFA indicated that individual wolves could be reliably discriminated primarily on the basis of the fundamental frequency of howls and the variability of frequency within howls. Yet, the relationship of these features with the individual wolves' body masses is not mentioned.

In defining a vocal signature, it is assumed that there has been selection for an effective mechanism of individual recognition, and discrete patterning in n 'th dimensional signal space is predicted. Of equal importance is that there should be no predictable nonrandom patterning or overlap among and between individuals i.e. this patterning should not be representative of simpler considerations of body mass, sex or ambient conditions. While selection may act on a recognition system by elaborating the cues that once functioned as a mass-based signal and now function in individual recognition, it should be evident that mass alone can no longer explain the measurable distinctiveness of individual cues in signal space.

The importance of this consideration will be illustrated in a hypothetical example : first, imagine the vocalisations of half a population (total size = 20) are recorded, and the pattern of similarity between and within individual vocalisations are analysed using a standard multivariate procedure (e.g. DFA). Vocalisations are described in five functional parameters, each parameter is found to be individually distinctive (i.e. inter-individual variability is greater than intra-individual variability), but with a little overlap in these 10 discrete groupings. The other 10 individuals from the same population are now included.

It will be found that either (1) that the overlap increases, and that there are no longer 20 discrete groupings. A continuum might emerge in one or a number of dimensions if these groups blend in a nonrandom way. Examination of the canonical discriminant functions might reveal that this patterning is suitably explained by something like body mass. If this is the case, then it is expected that this relationship will be present before the addition.

Alternatively, it may be found that (2) there is no overlap, and 20 discrete groupings are now present. When the other 10 samples were incorporated, the pattern of variability within each individual's signal space was not large enough to produce significant overlap with the pre-existing pattern of signal distinctiveness in the first 10 groups. Moreover, examination of the canonical discriminant functions would reveal that this patterning bears no significant relationship with mass or sex (although there is a real possibility that it may).

Now given that the hypothesis of signature individuality is being testing, the findings of (1) cannot be used to support a signature hypothesis. In such cases, it is more appropriate to seek a more parsimonious explanation for the function of the signal (see below). Conversely, it is expected that selection for a 'signature' will produce the outcome evident in (2). It is argued that the conditions in which a 'signature' needs to be invoked are likely to be rare.

Several researchers have attempted to statistically control for confounding factors in their analyses of variation in vocalisations. Weary *et al.* (1990) used a general linear model to study the residual variance after features (time of day, yearly differences, song type) that could obscure differences between the individual calls of great tits (*Parus major*) were removed. Age was found to be a main effect in an analysis of variance in an investigation of echolocation calls of the greater horseshoe bat (*Rhinolophus ferrumequinum*) (Jones & Ransome 1993). The patterning of the vocalisations of pipistrelle bats (*Pipistrellus pipistrellus*) during post-natal growth in discriminant space was qualitatively compared at two stages (day 6 and day 15) (Jones *et al.* 1991). Different parameters used in the discrimination were seen to change with age, and discrimination improved as the bats aged. Masters *et al.* (1995) incorporated age-class (juvenile-adult) and sex as two two-level factors in an analysis of variance of the sonar signals of big brown bats (*Eptesicus fuscus*). The results showed that adults differed significantly from juveniles, but no gender differences were evident. Sayigh *et al.* (1995) found that sex differences in the whistles of bottlenose dolphins (*Tursiops truncatus*) were extracted by analysing human judgements of the similarity of spectrograms. The most vigorous approach to date has been that of Scherrer and Wilkinson (1993) in investigating evening bat (*Nycticeius humeralis*) isolation calls. Here age was entered as a covariate into multivariate models and these revealed

significant variation in individual pup calls, showing that the linear effects of spectral variation of the calls with age could not account for the discrete patterning in multidimensional space. Furthermore, a split-plot analysis showed sex differences were not significant in the analyses.

All other studies reviewed (Tables 3.1 and 3.2) have overlooked the possibility of covariation with morphological traits and meteorological variability and its signature-masking potential. It is therefore appropriate to implement a more stringent set of criteria which must be met before invoking signature status and inferring an individual recognition function for a communication signal.

3.3.4 A methodological solution

There is a well regarded body of statistical theory that can be used to examine the influence of covariation on residual overlap between n 'th dimensional groupings, and therefore test whether these covariates are of significant interest (e.g. Rao 1966). DFA is probably the most useful approach in testing for vocal distinctiveness. However, other ordination techniques may be equally applicable. Most studies consider the patterning of n descriptor measures in n 'th dimensional space.

If the discrimination between individuals is explained by, for example, a phenotypic trait alone (e.g. mass), then one would expect a single significant canonical function that is perfectly correlated with the individual's masses. Visual inspection of canonical plots should also reveal if sex differences are extracted by the analysis. If there are a number of significant canonical discriminant functions, then it is likely that several explanations exist for the discriminant patterning (e.g. mass, or signature patterning).

A test of the influence of each potentially confounding covariate in the discrimination would simply be to plot each individual's mean score of the canonical variates against the respective values of the variable in question to see if there is any *a priori* evidence of a

linear relationship. If such a relationship is found, then this influence needs to be incorporated into the analysis model before useful interpretation can be offered. The fact that the covariate will often have zero within-group variance in the DFA (e.g. mass does not vary within individuals) means that this problem is taken slightly out of the usual realm of covariate-adjusted DFA (*sensu* Rao 1966, McLachlan 1992).

A profitable approach here would be to regress each of the descriptor measures on the variable of interest (in this case, a phenotypic trait). The residuals from each regression could then be pooled and used as the matrix in the DFA. If there is still 'good' discrimination, this is direct evidence that there is more to the patterning in discriminant space than could be predicted based on each descriptor measures' covariation with the phenotypic variable. If the discrimination, which was initially successful, changes significantly and loses its discrimination potential, this is evidence that most of the discrimination is due to the phenotypic variable in question. If this is the case, it is more parsimonious to invoke less restrictive explanations than 'signature' explanations.

It is suggested that if an analysis depicts patterns of variation that can be adequately accounted for by phenotypic characteristics (e.g. mass or sex differences), or by covariation with extraneous variability (e.g. temperature or humidity fluctuations) then it is sensible to avoid the invocation of a signature function.

3.3.5 The playback paradigm

Cue isolation experiments allow for the precise testing of the function of a communication signal because the possible influence of other potential cues are controlled. Acoustic playback and phonotaxis experiments have been used extensively in the study of anuran (reviewed in Arak 1983, Ryan 1985, Gerhardt 1994) and avian (reviewed in Falls 1982) communication systems. In frogs it is apparent that various call parameters can covary with body mass; here indeterminate growth would result in considerable size-related signal

variation within the adult population. Higher vertebrates show determinate growth but nevertheless considerable size variation amongst adults (e.g. Clutton-Brock *et al.* 1982).

Communicating size as an honest signal is ubiquitous and may influence mate choice, if this information is encoded in a sexual signal. There is a substantial body of evidence confirming predictable covariation in body size with spectral and temporal characteristics of vocalisations for taxa across all vertebrate classes: fish (e.g. Myrberg *et al.* 1965, Myrberg & Riggio 1985), amphibians (e.g. Davies & Halliday 1978, Ryan 1980), reptiles (this study), birds (e.g. Schubert 1976, Lanyon 1978, Eens *et al.* 1991), mammals (Marler & Hobbett 1975, Clutton-Brock & Albon 1979). Nevertheless, the playback experiments reviewed in the present study (Table 3.2) have each failed to control for the possible influence of size-based signal variation on the responses of test subjects. This problem is well illustrated in two studies of neighbour recognition in a coral reef fish (Myrberg & Riggio 1985), and in a frog (Davis 1987). Both studies report positive neighbour discrimination yet fail to mention any control for the size-based effects on call frequency in the stimuli they used in playback experiments. This is despite the fact that the low frequency calls, characteristic of the largest most competitive males, are often the most attractive to females.

A relatively recent approach focusing on the interest of birds as receivers and interpreters of song (*sensu* McGregor 1991) is that of operant conditioning playback techniques (Park *et al.*, 1985, Park and Dooling 1985). These techniques allow researchers not only to identify how stimuli differences are perceived (i.e. discrimination), but also how different stimuli are grouped (i.e. categorisation) (Weary 1990). Through ingenious experimental procedures researchers have been capable of testing the perceptual capabilities of several bird species. Weary (1990) used operant procedures to determine which acoustic parameters great tits (*P. major*) used to categorise song notes. Loesche *et al.* (1991) used similar techniques in an attempt to separate signature adaptations (where signal variability is maximised between individuals and minimised within individuals) from perceptual adaptations (natural selection acting on the receiver's perceptual capacity). Here operant techniques were used in a comparative investigation of the perceptual workings of two closely related species - the barn swallow (*Hirundo rustica*) and the cliff swallow (*H. pyrrhonota*). Stoddard *et al.* (1992) showed how memory does not constrain the individual

recognition capabilities of male song sparrows (*Melospiza melodia*) - a bird with song repertoires.

Although operant techniques may successfully demonstrate the perceptual capacity of animals for individual recognition, or identify the features of signals that are used by receivers - they do not always provide a sufficient understanding of the functional significance of the underlying mechanisms. Once again, it is supposed that this is of importance when testing hypotheses of information content (e.g. individual distinctiveness). For example, Weary and Krebs (1992) demonstrated how great tits (*P. major*) recognise the general voice characteristics of an individual's song repertoire. However, information about the obvious differences and phenotypic correlates between the song features of the two individual's voices used in the playbacks is not noted. Beecher *et al.* (1994) demonstrated how in song sparrows (*M. melodia*), voice characteristics (signature traits) are insignificant in song discrimination. The birds classify song according to song type, rather than by singer. The protocol used in this experiment overlooks the influence of size as a masking source in the operant conditioning playback stimuli - a factor that while probably minor if the song stimuli were sampled carefully from the singer population - could also severely confound interpretation of the results if they were not.

It is suggested that playback studies first need to establish the existence and extent of covariation in call structure with body size. Only if this is negligible can standard playback experimental protocols be employed. However, if covariation is substantial, then playback methodology must be modified to incorporate controls that distinguish between individual- and size-based discrimination. This is essential before a signature function may be invoked.

3.3.6 Theoretical implications

In a sample of 39 analytical studies and 45 experimental studies, only 12 species have been investigated using both analytical and experimental approaches to the study of individual recognition by voice, none of which meet the criteria for empirical verification of

a signature system. The validity of these two lines of evidence for the role of signatures in individual recognition are questioned from two broad stances:

1. Very few studies to date present convincing statistical evidence for the existence of signatures. This is not because they do not exist but rather because of a lack of consideration of the influence of variable phenotypic traits and extraneous variability on signal structure.
2. Playback experiments aiming to verify the existence of a signature function of a vocalisation are designed with the assumption that the vocalisations are individually distinct but not how (see 1 above). This assumption cannot be made until signature status is statistically verified. If this information is not available then playback experiments must include a protocol which controls for the effects of any size- or sex-based differences in signal structure.

It is argued that empirical verification of an acoustic signature requires two lines of evidence, both of which should routinely control for confounding phenotypic covariables:

1. multivariate statistical confirmation of signature status, and
2. experimental verification of the recognition function of the signal.

In a thorough literature search, no studies are recognized as meeting both these criteria. It must be concluded that acoustic signatures may be far less prevalent in animal communication repertoires than the literature leads us to believe.

3.3.7 A case study : the naked mole-rat and the barking gecko

Having adequately reviewed past approaches to the study of inter-individual variability in animal vocalisations, and having proposed a statistical method that is capable of controlling for incidental sources of variability, the logic of this refined approach is now demonstrated with an example in two vocal animals displaying remarkably different degrees of social elaboration.

It is understood that sophisticated communication repertoires often characterise extreme forms of social organisation (Seyfarth *et al.* 1980, Maier *et al.* 1983, Seeley 1985, Michener & Smith 1987, Linsenmair 1987). For example, mechanisms of nest-mate recognition are well established in the eusocial hymenoptera (Gamboa *et al.* 1986). Conversely, communicative elaboration is often less pronounced in social systems where signals have evolved to satisfy simpler functions, like those involved solely in territorial demarcation (Otte 1974). This prediction provides a strong *a priori* incentive for applying the methodology developed above in a case study of two animals that are expected to differ in the information capacity of their respective signals. The information content of vocalisations of the eusocial naked mole-rat and the territorial barking gecko are thus investigated.

Naked mole-rats

Naked mole-rats are highly vocal, with a repertoire of at least 17 discrete vocalisations, many of which are context-specific (Pepper *et al.* 1991). Of these, the soft-chirp call is clearly the most common vocalisation, and has been described as a quiet birdlike sound, reminiscent of the peeping of chicks (Pepper *et al.* 1991) (Fig. 3.3). This call is emitted immediately after two individuals have come into direct contact (personal observation) and also when individuals are isolated from their colony mates (or alone in a tunnel). Thus interactions within the colony most often commence with soft-chirping between individuals. A previous study reported clear variation in the structure of the soft-chirp between individuals, and also noted that all soft-chirps in one procession were similar in form (Pepper *et al.* 1991). Conspicuous differences were noticed between individuals in the form of variation in the soft-chirp (duration, frequency range, and extent of the upswing portion) suggesting the possibility of the soft-chirp functioning as an effective recognition mechanism.

Barking gecko

Behavioural observations suggest that the functional significance of the advertisement vocalisation of *P. kochi* lies in territorial maintenance and possibly mate-selection (Section 1). Experimental investigations have elucidated a clear role for sound intensity in inter-male spacing (Section 2). Whereas certain aspects of the gecko vocalisation are stereotypic and evidently different between individuals, an examination of call descriptors have revealed a high extent of covariation of these features with morphological and extraneous variability.

This suggests that the likelihood of these calls acting as an effective individual recognition mechanism between territorial males (*sensu* Falls 1982) is diminished. It is of interest to understand more about the information basis of these calls, and by so doing, aim to understand more about the biological significance of these vocalisations.

3.3.7.1 A note on receiver psychology

Approaching an understanding of communication systems from the basis of a third-party observer (rather than the receiver) suffers from the same problems as the original application of Shannon-Weaver ideas to communication - receiver psychology is implicitly ignored. Guilford & Dawkins (1991) have pointed out that receiver psychology is vital to an understanding of the form of signals and signalling behaviour. Consequently, inferences about the signature properties of a signal cannot be made until the receiver abilities have been investigated. It is argued that the empirical verification of an acoustic signature requires two lines of evidence, both of which should control for confounding covariables (i.e. multivariate statistical confirmation of potential signature status, and experimental verification of the recognition function of a signal). A full analysis of individual distinctiveness can therefore be seen as the first essential step in any investigation of the variability manifest in a communication system.

The past 30 years has witnessed a plethora of studies aimed at identifying the acoustical bases for individual recognition cues solely through the use of analytical methods. The ideas presented in this section (Section 3.3), although focused on the analytical aspects of understanding the bases of individual voice variation, do not deny the importance of the study of receiver properties. Rather, this work is aimed at correcting an ongoing tradition of analytical error in this preliminary stage of an investigation into the functional significance of individuality in signal communication.

3.3.8 Methods : generalised linear models and covariate-adjusted discriminant-function analysis

Data Analysis : General

Each species' call was decomposed into a number of descriptor measures. Each descriptor measure vector was tested for normality and transformed if necessary. Tests of repeatability, distribution-fitting and general-linear modelling (GLM) were performed using Systat statistical software (SYSTAT 1992). DFAs were run on Statistica (STATISTICA 1995) and cross-validated using Statgraphics statistical software (V 6.0, STATGRAPHICS 1992).

When investigating the differences in intraspecific patterns of variation between individual vocalisations, single variable approaches to examine patterns of this variation are unrealistic - there may be no single acoustic character that sufficiently encapsulates the differences between individuals. Multivariate analyses are clearly more appropriate in investigating the patterns of variation between individual's vocalisations. Multivariate analysis of variance (MANOVA) and, more important, DFA techniques provide a powerful quantitative tool for examining the shape and nature of inter-individual acoustic phenomena. DFA has proven to be a particularly robust analytical technique (able to produce valid conclusions in the face of invalid or deviant initial assumptions) as long as sampling techniques cater for group sizes that are large and equal (Pimentel & Frey 1978). Furthermore, DFA is affine invariant (therefore is not affected by problems of multicollinearity between descriptor measures) (Eaton 1988). It has been suggested that interdependencies between descriptor measures could complicate interpretation of DFA results (McGregor & Byle 1992). The correlation between descriptor measures is, in fact, irrelevant. It may seem sensible that ordination techniques should be used to rotate the descriptor measure matrix to uncorrelated dimensions before using these values in DFA (e.g. Beecher 1989). This is not only inconsequential but in fact prejudicial to the final results as information may be undoubtedly lost if components 'deemed to be unimportant' are dropped from the analysis. Canonical discriminant-functions having eigenvalues less than one can be assumed to be redundant with respect to variance information (Jobson

1992). Hence, a lower bound is set in interpreting the number of resultant discriminant functions displaying eigenvalue structures greater than one.

Data Analysis : naked mole-rats

A pseudo-random sample (displaying a representative range in body mass) of 11 *H. glaber* individuals (6 females, 5 males) from one pure-bred Northern Kenyan captive colony were sexed and weighed, and subsequently used in recordings. Each animal was placed in isolation under constant temperature and humidity conditions in an anechoic chamber until 30 clear calls were emitted. Each soft-chirp recording was made and digitised according to the same protocol outlined in Section 3.1 (General methods and materials). Sonagrams were decomposed into a number of descriptor measures. These were : DUR (duration), TTP (time to peak), UFQ (upper frequency), LFQ (lower frequency), PKFQ (peak frequency), ϕ (angle of downslope), δ (angle of upslope) (Fig. 3.3). In a sample of 27 calls from 11 individuals, all physical measures were significantly and highly repeatable (*sensu* Lessells & Boag 1987) (DUR: $r = 0.928$, $F = 26.789$, $d.f. = 26,27$, $P < 0.000$; TTP: $r = 0.982$, $F = 109.939$, $d.f. = 26,27$, $P < 0.000$; PKFQ: $r = 0.977$, $F = 87.435$, $d.f. = 26,27$, $P < 0.000$; UFQ/LFQ: $r = 0.996$, $F = 580.409$, $d.f. = 26,27$, $P < 0.000$). Acoustic indexes of the descriptor measures were created where necessary. The selection is again arbitrary, and is based on the necessity to quantify those features that appeared from visual inspection of sonagrams to distinguish soft-chirps between individuals. These were: (1) Duration of the pitch profile in ms (DUR), (2) time to peak frequency (TTP), (3) Relative peak position (RPP) of peak frequency relative to the whole pitch profile (0 - beginning ; 1 - end), (4) Peak frequency in KHz (PKFQ), (5) Frequency range (PKFQ - LFQ = FQR), (6) Slope symmetry (SS) - the difference between averaged slope angles ($\phi - \delta$), (7) Duration symmetry (DS) - the difference between the duration of downsweep ($\sqrt{\{[DUR-TTP] + [PKFQ - \text{End frequency}]\}}$) and upsweep ($\sqrt{\{TTP + [PKFQ - \text{Starting frequency}]\}}$), and (8) A generalised index of tonal symmetry (RELXY) ($\{1 - (\text{duration upsweep} / \text{duration downsweep})\} \times 10$). Three vectors required transformations to satisfy the condition of multivariate normality.

Thirty 8-dimensional vectors for each individual were used in the initial DFA. If the discrimination between individuals in this first analysis could be explained by mass alone, then only one significant canonical discriminant-function (which would be perfectly correlated with the individual's masses) would be evident. This was not the case. However, when the values for

each individual's mean score on the canonical functions were plotted against mass, canonical discriminant-function one revealed a linear relationship with mass (Pearson r : $r = 0.584$, Bartlett $\chi^2 = 3.542$, d.f. = 9, $P_{\text{(one-tailed)}} = 0.029$). Hence, mass is influencing the patterning in the first discriminant dimension in a significant way. A covariate-adjusted DFA approach was used to control for the influence of this mass based covariation on the spectral measures : each descriptor measure vector was first regressed on mass. The residual vectors from each regression were then pooled and used as the matrix in the now covariate-adjusted DFA (Rao 1966, McLachlan 1991).

Data analysis : barking gecko

Sampling numbers and recording techniques are outlined in detail in Section 3.1 (General methods and materials). The sample of 300 calls (15 individuals, 20 calls each) was used in this analysis, each call being separated into the same five descriptor measures (see Section 3.1; Fig. 3.1). DUR and CLICK are autocorrelated variables (Section 3.2.1). While DFA results would be unaffected by the inclusion of both of these measures (being affine invariant), the composite index (DOC) is used to simplify the analysis. The vector BCI required a log-transformation in order satisfy the condition of multivariate normality in the 300 4-dimensional (descriptor) vector data set.

Morphological features (extent of yellow coloration, mass and length) and average SPL for any one male, as well as several meteorological variables, were treated as potential covariables (see Table 3.3). General meteorological variables were noted from the research station's weather station for each recording session (of any one male). The research station provides dependable morning, afternoon and evening recordings of certain meteorological variables. Several of these were used as potential covariates : dry-bulb temperature at 14h00 hours, dry-bulb temperature at 20h00 hours, relative-humidity at 20h00 hours, windspeed, night-minimum temperature, and soil temperature at 5 cm, 10 cm, 20 cm and 30 cm below the sand surface. The values of temperature and humidity recordings on site (inter-dune spaces) were compared to those of the weather-station (gravel plains) - no microhabitat effect was found to be significant in these two variables (temperature: $r = 0.980$, d.f. = 20, $P < 0.000$; humidity: $r = 0.960$, d.f. = 20, $P < 0.000$).

In an attempt to control for any covariance between call characteristics and morphological/meteorological variability, a process of stepwise multi-factorial GLM analysis was performed. First a descriptor measure was entered as the dependent variable, and all morphological (total four) or meteorological (total ten) variables were entered as factors (see Table 3.3). All order five and lesser interactions between the factors were included (e.g. {A x B x C} would be a third-order interaction, where the factors A, B and C were not 'independent' of the presence of a particular 'level' of any of the other two factors). The GLM model included predictor variables in a stepwise process (tolerance = 0.01, $\alpha \geq 0.15$ for removal). The resultant model presented a unique set of independent variables that was best able to partition the variance associated with the descriptor measure (Table 3.4). The residuals from suitable models were stored and used in the subsequent (covariate-adjusted) DFA analyses. All models utilised were confirmed for model fit by examining the assumption of homoscedascity in the residual scatter.

This process was repeated for each descriptor measure. First the influence of morphological covariation was eliminated. The residuals from these analyses formed the 20 4-dimensional vectors for each individual that were used in the DFA (now adjusted for morphological covariation). Second, this residual matrix was used in a second GLM analysis where it was attempted to control for the effects of meteorological covariation. Here each of the descriptor measure scores (adjusted for morphological covariation) was entered in turn in the GLM analysis. The residuals from these analyses forms the 20 4-dimensional vectors for each individual that were used in the final DFA (now adjusted for both morphological and meteorological covariation).

3.3.9 Results

Naked mole-rats

The DFA on the raw data shows four significant discriminant functions having eigenvalues greater than one (Table 3.5). These explain over 95% of the total variance in the 8-dimensional matrix structure. Canonical discriminant function one loads heavily on PKFQ and FQR, function two mostly on RPP but also on FQR, DUR and TTP. Function three loads almost equally on

DUR, TTP and RPP. Function four loads mostly on TTP and then RPP and DUR (Table 3.6). Percent correct classification ranged from 83% to 100% with the average success on resampling being 93% (9.09% predicted by chance alone). A plot of bivariate centroid 95 % confidence intervals around each individual set of repeated measures for the first two canonical discriminant axes shows how the groups are individually distinct (Fig. 3.4). Visual inspection of significant canonical discriminant-functions reveal that sex differences are not emphasised by the analysis.

When the DFA is repeated, this time using the adjusted scores for each of the descriptor measures (the residuals of the linear model of each descriptor measure regressed on mass), the first three significant discriminant functions have eigenvalues greater than one (Table 3.5). These explain over 92% of the total variance in the 8-dimensional matrix structure. Canonical discriminant function one loads heavily on PKFQ and FQR, function two and function three load almost entirely on FQR and DUR (Table 3.6). Percent correct classification ranged from 80% to 100% with the average success on resampling being 88% (9.09% predicted by chance alone). The plot of individuals groupings in discriminant signal space for canonical discriminant functions one and two shows how the patterning between individuals changes slightly, but the groups remain individually distinct (Fig. 3.4). Inspection of significant canonical discriminant-functions reveals that sex differences are still not emphasised by the analysis.

The results show that the soft-chirp is highly distinctive within individuals in discriminant signal space. However, although these discrete signals display considerable individual call stereotypy, this is unconstrained by the influence of size- and sex-based covariation. The fact that there is appreciable discrimination is direct evidence that there is more to the patterning in discriminant space than could be predicted based on each descriptor measures' covariation with mass.

Barking geckos

The results from GLM expose the degree to which several call characteristics predictably covary with morphological and meteorological factors (Table 3.4). It is here that the existence of more effective predictors of vocalisation features can be observed through the use of composite morphological and meteorological measures. Apart from AFREQ - now described by a unique linear combination of morphometric measures - the GLM selections show that

morphological indexes explain little more than each morphological measure on its own (see Section 3.2.5). On the other hand, linear meteorological composites are better able to partition the variance associated with call descriptor measures (see Table 3.4). The GLMs result in appreciable meteorological predictors of AFREQ ($R^2 = 0.500$) and RANGE ($R^2 = 0.222$). The GLMs also refine the prediction of DOC ($R^2 = 0.722$) using weather composites.

DFA on the original data gives three significant discriminant functions having eigenvalues greater than one (Table 3.7). These explain over 99% of the total variance in the 4-dimensional matrix structure. Canonical discriminant function one loads heavily on AFREQ, function two on DOC and function three loads on RANGE (Table 3.8). Percent correct classification ranged from 15% to 100% with the average success on resampling being 72% (6.66% predicted by chance alone). The plot of bivariate centroids around each individual set of repeated measures for the first two canonical discriminant axes shows how the groups are individually distinct (Fig. 3.5).

The DFA for the scores adjusted for the covariation of call structure with morphological variables displays only two significant discriminant functions have eigenvalues greater than one. These explain over 96% of the total variance in the 4-dimensional matrix structure (Table 3.7). Canonical discriminant function one loads heavily on AFREQ and function two on DOC (Table 3.8). Percent correct classification ranged from 0% to 100% with the average success on resampling being 70% (6.66% predicted by chance alone). The patterning in discriminant signal space shows how the groupings begin to coalesce (Fig. 3.5).

DFA performed on the scores adjusted for both morphological and meteorological covariation with call structure, indicates that only the first significant discriminant function has an eigenvalue structure greater than one (Table 3.7). This explains only 62% of the total variance in the 4-dimensional matrix structure. Canonical discriminant function one loads heavily on AFREQ (Table 3.8). Percent correct classification ranged from 5% to 90% with the average success on resampling being 34% (6.66% predicted by chance alone). The groupings in discriminant signal space clearly mix with each other (Fig. 3.5)

3.3.10 Discussion

Naked mole-rats

Eusociality in insects and naked mole-rats is an intriguing mix of cooperation and conflict (Lacey & Sherman 1996). The extremely low levels of variability in naked mole-rat DNA in normally highly polymorphic loci suggests that this species has little or no genetic diversity (Faulkes *et al.* 1990, Reeve *et al.* 1990). However, this does not preclude the appearance of clear forms of nepotism or aggression in this species (Reeve & Sherman 1991, Reeve 1992). Reproduction in any single colony is usually limited to one female and one to three breeding males (Jarvis 1981). The breeding females tend to be the most dominant (Lacey & Sherman 1991).

The breeding female is one of the heaviest individuals in the colony (Lacey & Sherman 1991), yet overall, size is not a reliable predictor of age in the naked mole-rat (Jarvis *et al.* 1991). Non-breeders cooperate in colony maintenance, foraging and defence (Jarvis 1981, Lacey & Sherman 1991). It has also been stated that the single breeding female initiates inherently lazy workers (which tend to be the larger and less related to herself than smaller worker individuals) by shoving them (Reeve 1992, *c.f.* Jacobs & Jarvis 1996). Her overt aggression is responsible for behavioural castration of nonreproductive individuals (Reeve 1992). Agonistic encounters among nonbreeding individuals over food and digging sites are commonplace (Reeve & Sherman 1991), and recently, the existence of a size-based dominance hierarchy has been established (Schieffelin & Sherman 1995). Here, heavier individuals gain preferential access to food through their competitive superiority in tugging contests. The same animals are also thought more likely to obtain breeding opportunities.

It is theoretically plausible that the long-term maintenance of a dominance hierarchy is sufficient for the evolution of a mechanism for class or individual discrimination (Barnard & Burk 1979, Dawkins & Guilford 1991) and selection for a mechanism that is immune to cheating (Zahavi 1975). Individual naked mole-rats could have adopted honest signalling of competitive ability to appraise asymmetries and thus dictate the pattern for the escalation of encounters. The assessment of the probable outcome of future encounters (memory) is likely to be the best way

of economising energy and risk of injury (Barnard & Burk 1979). A signal used in mutual assessment is likely to comprise as many cues, and whatever degree of cue elaboration as is required to make such a mechanism reliable and honest.

The results reveal appreciable individual distinctiveness in naked mole-rat soft-chirps; this being independent of size and sex (Fig. 3.4). There would be an element of redundancy in the signal if it were used solely as a body-size cue in a size-based dominance hierarchy. Unless a size-based signal is especially open to cheating in naked mole-rat colonies, the elaboration manifest in the soft-chirp must be illustrative of other selection pressures.

The soft-chirp may function as an honest signal of status in a size-based dominance hierarchy. However, a size-based hypothesis is insufficient to explain the evolution of a vocal signature because the information potential would be vastly under-utilised.

It would be profitable for researchers to establish the exact functional significance of the soft-chirp by playback experiments. If it is assumed that the soft-chirp signal, because of its distinctiveness, may be functioning (*sensu* Williams 1966) as a signature, then several interesting possibilities exist for its evolutionary significance. Naked mole-rat research has emphasised investigation into colony-level patterns, but non-random patterns of association between individuals has been neglected. Given that individual recognition by voice is a possibility (c.f. O'Riain & Jarvis 1997), aspects of naked mole-rat behaviour need to be investigated in more detail. The novel observation that the naked mole-rat possesses the features of a vocal signature should provide continued incentives for understanding the importance of kin-selection (Hamilton 1964) and previously unconsidered selective forces (e.g. reciprocity) that are manifest in the social organisation of this enigmatic mammal.

Barking geckos

The non-covariate-adjusted DFA of barking gecko calls suggests individuality of signal structure, but subsequent analyses removing the effects of morphological covariables and meteorological covariance render the calls statistically indistinguishable from one another (Fig. 3.5). This is clear evidence against the potential for advertisement calls of the barking gecko functioning as vocal signatures. Here selection appears to not have favoured the evolution of a mechanism for

individual recognition, perhaps because of the combined constraints of morphology and ambient conditions on signal structure.

In some birds that advertise territory occupancy through song, territory owners have the ability to distinguish between the songs of neighbours and other conspecifics; a phenomenon known as neighbour-stranger discrimination (Falls 1982). Here discrimination can be achieved using only the information encoded in the song. Selection has probably not favoured the evolution of a similar mechanism of discrimination in *P. kochi*, as male calls are clearly not statistically distinguishable. Furthermore, playback studies have revealed a congruent set of phonotactic responses that are consistent with a parsimonious competition model based on sound intensity (Section 2.4.3). There seems to be, therefore, no *a priori* basis for searching for an alternative explanation. However, the prediction that neighbour-stranger discrimination does not occur in *P. kochi* remains to be experimentally verified.

3.3.11 Conclusions

It is easy to envisage a range of benefits associated with the evolution of a vocal signature in group-living organisms characterised by extreme forms of social organisation (Beecher 1982). Any form of social organisation reliant on reciprocity and nepotism is likely to be coupled with the evolution of individual group member recognition (see discussion of naked mole-rats above). Similar sources of selection are not predicted to be apparent in most solitary and group-living species. Nevertheless finer sources of selection can generate differing degrees of individual recognition; for example neighbour-stranger discrimination in territorial songbirds (Falls & McNicholl 1979, Godard & Wiley 1995).

The work presented here serves to illustrate the robustness of a statistical procedure designed to support or refute the potential existence of a vocal signature. A case study on the soft-chirp of *H. glaber* reveals how this call is highly distinctive within individuals, and how this distinctiveness is unrelated to morphological covariation. A similar investigation of the advertisement vocalisation of *P. kochi* reveals how once morphological and meteorological

covariation has been statistically removed, the calls are statistically indistinguishable from one another. This study presents strong evidence for the potential of the *H. glaber* soft-chirp functioning as a vocal signature, and suggests the likelihood of the *P. kochi* advertisement call functioning as a signature is minimal. Only through rigorous comparative testing using similar covariate-adjusted approaches in many different animal systems can the possibilities of acoustic signatures evolving convergently under similar social selection pressures be elucidated.

3.4 Modelling chorus activity

As was demonstrated in Section 3.3.8, many aspects of vocalising in *P. kochi* are profoundly affected by ambient sources of variability (see Table 3.4). Here chorus activity is similarly examined. Evening choruses typically last 50 minutes, but extend disproportionately when there is clear spike (high) in temperature. Strong windspeeds (greater than 7 m/sec) preclude chorus activity altogether. The occasional north-west wind in the central Namib desert also results in a cessation of calling activity. This condition results in a combined influx of cool air (less than 19 °C) and medium to strong winds (greater than 5 m/sec).

Understanding the predictability of nightly chorus behaviour by considering its covariation with meteorological factors is of fundamental interest. External factors are known to be significant in influencing both the onset and duration of chorusing behaviour in some species of anurans (Blakenhorn 1972). Similarly, understanding how dependent the chorus duration of *P. kochi* is on external sources of variability is potentially answerable, as reliable measures of both chorus behaviour and meteorological variables have been recorded. Here chorus behaviour is modelled in an attempt to identify the primary factors that account for nightly variation in chorus duration.

On site observations were made over 104 evenings, of which 74 (71 %) exhibited chorusing behaviour. As noted in Section 3.3.8, several meteorological variables were noted for each evening's recording session from the research station's weather research

station. The subset explored here were : 14h00 dry-bulb temperature (DBT), 20h00 DBT, relative humidity at 20h00, wind speed at 20h00, wind direction at 20h00, 20h00 soil temperatures at 5 cm, 10 cm, and 20 cm, and night minimum temperature. Due to missing weather observations, 63 days presented complete records of these variables.

The starting times and temperatures and ending times and temperatures of choruses were noted for each evening. The chorus duration of any evening was calculated as the difference in minutes between starting and ending times of an evening chorus. The change in temperature within an evening's chorus is computed as the difference in degrees Celsius between the starting and ending temperature. Effective moonlight in the study area was quantified as a continuous variable ranging from 1-9 (1 - no moonlight present, 5 - half moon lighting, and 9 - fullmoon lighting). The difference in temperature between the 14h00 DBT and the night minimum readings was termed the decay range. The time sequence of chorus evenings throughout the study period was coded on a daily basis. Wind direction has a circular scale of measurement and cannot adequately be accommodated in the regression model. This variable is thus left out. 11 predictor variables of duration (see Table 3.9 for summary) are used in the multiple-regression analysis.

3.4.1 Model selection : forward stepwise multiple-regression

The objective of multiple-regression analysis is to find a linear equation that predicts the variance associated with the response variable (in this case chorus duration) in these presence of other explanatory variables (here the 11 predictor variables mentioned above). However, there are several possible complications in such an analysis, and these should be conferred to avoid misinterpretation. First, multicollinearity (intercorrelations) among the predictor variables compromises the predictive power and interpretability of the analysis (Carnes & Slade 1988). In this study, it is likely that several of the predictor variables are highly correlated with each other. The stepwise-procedure has a safeguard against singularity (called the tolerance level - L) that precludes the entry of predictor variables whose R^2 value with others (already included in the model) exceeds $1 - L$. This should

eliminate a large degree of predictor redundancy. The extent of multicollinearity in the final model can be gauged by examining whether or not the error terms in a regression model are autocorrelated (Neter *et al.* 1988). Here, the Durbin-Watson test is used to test the extent of first-order autoregressive error.

Second, it is meaningful to understand that only in situations where the predictor variables are controlled by the investigator can the individual coefficients of the resultant multiple-regression equation be interpreted as the 'effect' that each predictor variable has on the response variable. This was not the case here, and the coefficient weightings must therefore be interpreted with care.

Lastly, and perhaps most importantly, stepwise regression procedures do not rank variables by their importance, and are therefore not effective in screening variables that may improve prediction. Hence, stepwise analysis might be confounded by the order in which variables are entered into the model. Stepwise analysis may also eliminate variables that are important. It is well understood that, for a given data set, stepwise regression selection will not necessarily find the best fitting model or even alternative plausible models (James & McCulloch 1990). The best that can be hoped for is that the stepwise procedure will select a subset of variables that does an adequate job of prediction (Sokal & Rohlf 1981).

The frequency distribution of the duration vector shows no significant departure from normality (Kolmogorov-Smirnov goodness-of-fit test, $D_n = 0.101$, $P = 0.116$) and therefore requires no transformation. Duration was entered as the response variable, and the 11 predictor variables were entered as independent variables into a forward stepwise regression model. The minimum tolerance for entry into the model is set at 0.100. An alpha level of significance for entry or removal of a predictor in the forward stepwise process is set at 0.150.

3.4.2 Results and discussion

The best subset model includes 6 out of the 11 predictor variables. Together, these explain 76.6% of the variation associated with chorus duration. All predictors are statistically significant except for the constant (intercept) value included in the resultant regression equation (see Table 3.9 for significance values).

The best subset model is represented by the equation :

$$\begin{aligned} \text{duration} = & 0.137(20\text{h00 DBT}) + 0.459(\text{relative humidity}) - 1.785(\text{windspeed}) - \\ & 1.575 (20 \text{ cm soil temperature}) - 0.433(\text{time}) - 5.146(\text{change in} \\ & \text{temperature}) + 10.525 \end{aligned}$$

The pattern of variation of chorus duration is extraordinarily well accounted for by the model's selection of these 6 meteorological variables ($R^2_{\text{adj}} = 0.776$, $F = 15.260$, d.f. = 6,56, $P < 0.000$). The Durbin-Watson D statistic is computed as 1.422, and the probability of a first-order autoregressive error is estimated to be unimportant ($P = 0.732$). Chorus behaviour is therefore seen to display a marked dependency on several meteorological variables and chorus duration tracks the fluctuations associated with these variables in a wholly predictable fashion. Although the coefficient weightings should be viewed with discretion, the results from the multiple-regression analysis suggest that temperature is the most influential causal mechanism behind understanding the variation in nightly chorus duration (displaying consistently heavier weightings). While the model selection performed here can help develop causal hypotheses about the nature of chorus duration dependency - the verification of these ideas will require some form of controlled experimentation.

3.5 Vocalisation conclusions

This section has approached the study of gecko vocalisations through a supplication to the usefulness of the concepts inherent in information theory. The fundamental theme has been one of comprehending the nature of the covariance of individual vocalisation features with both extraneous and intrinsic factors. Only by statistically controlling for incidental sources of variation can the uncertainty associated with call features be minimised, and possible (initial) biological hypothesis be offered for their relevance.

The variance and covariance of *P. kochi* call descriptor measures were initially explored in order to emphasise the sonographic features that appeared to distinguish calls between individuals. The temporal descriptor of between-click interval was seen to be informatively obsolete as it was clearly predictable based on the click number and duration of any call (Section 3.2.1). The multiple-harmonic structure of calls were investigated in an attempt to assess the practicability of summarising the variance associated with the emphasised harmonic banding of vocalisations. The index AFREQ, obtained by averaging the mid-frequencies of both the wide- and narrow frequency bands was seen to be an adequate predictor of the patterns of variation in either band (Section 3.2.2).

Call duration (DUR) and call rate (BCI) were seen to slow down with the corresponding decrease of ambient temperature. The decrease in call duration was seen not to decline any differently than could be predicted based on the observed changes in ambient temperature. Once the covariance of call duration with temperature was statistically removed, individuals displayed no significant differences in call duration (Section 3.2.3). Call rate was similarly examined. The degeneration of call rate was weakly influenced by the effect of temperature, and individuals' call rates decayed at significantly different rates, independently of the effects of temperature (Section 3.2.3). The implications of this finding are discussed more fully later (see Section 4.1).

The number of clicks present in the vocalisations of the barking geckos is a historically entrenched taxonomic feature often used to separate the species of *Ptenopus* (Haacke 1969,

Branch 1988). The degree of spread of click number manifest in a large recording sample of *P. kochi* was examined. The range in click number for *P. kochi* was found to overlap with that documented for *P. garrulus*. However, click number was seen to be independent of ambient temperature conditions (Section 3.2.4). It is expected that this level of overlap will not become appreciable with temperature changes. The importance of this will be further discussed in Section 5.1.

Other relationships between call descriptor measures and morphological and temperature measures were considered. Several significant linear correlates were found, but the general strengths of these relationships were surprisingly weak and unconvincing (Section 3.2.5). GLM techniques were employed in an attempt to find more effective predictors of call features using linear combinations of morphological and meteorological measures. The results from these models reveal the degree to which several call characteristics predictably covary with these composite measures (Table 3.4). The variance of descriptor measures duration/click (DOC) and frequency range (RANGE) was largely explained and the descriptor of average frequency (AFREQ) was reasonably well accounted for. The variation associated with the call descriptor, between-call interval (BCI), remains almost entirely unaccounted for. In general, meteorological covariation explained the majority of the variance in the call descriptors.

In order to better understand the notion of the unexplained (residual) variance associated with call descriptor measures, the conceptual framework of information theory was introduced and discussed. A covariate-adjusted approach to DFA was found to be a workable statistical tool for the examination of these incidental sources of variation, and for distinguishing between individual- and extraneous-based sources of variation. The information content of the vocalisations of both *H. glaber* and *P. kochi* was investigated in a case study in order to illustrate the utility of a covariate-adjusted approach. Results from these analyses revealed how individual *H. glaber* soft-chirps displayed appreciable individual call stereotypy that was highly distinctive in discriminant signal space and independent of both size- and sex-based covariation (Table 3.5; Fig. 3.4). Call patterning in *P. kochi* was seen to covary reliably with both morphological and meteorological determinants (Table 3.4). However, once this predictable variation was eliminated from signal space, there was no substantial information remaining in the gecko calls that could afford it unique individual distinctiveness (signature) status (Table 3.7; Fig. 3.5).

These findings are congruent with predictions regarding the information capacity of signals and its relation to social function. This research therefore demonstrates clearly the inherent feasibility of covariate-adjustment in studies of communicative information where information explanations are analytically explored.

Lastly, chorus activity was statistically modelled using a forward stepwise multiple-regression analysis in order to discern whether, like many other facets of *P. kochi*'s vocalisations, variation in nightly chorus duration was predictable. Several meteorological determinants displayed a sizeable degree of covariation with chorus duration, and the pattern of variation of nightly chorus duration was explained by these predictors (Table 3.9).

Theoretical considerations suggest that signalling used to convey information about contest ability is sufficient for the evolution of a form of class or individual discrimination (Barnard & Burk 1979). Such a signal also needs to be honest if it is to be evolutionarily stable (Zahavi 1975, Grafen 1991). As has been mentioned, males of *P. kochi* adjust their activity on a diel basis so that they signal at the same time as their neighbours (see Section 2). The acoustic signals produced by *P. kochi* exhibit collective patterning of temporal signal interactions, where vocalising males alternate their acoustic interactions with neighbouring males. While several non-adaptive explanations exist for this behaviour (Greenfield 1994), the hypothesis that individual animals chorus and exhibit alternating signal displays to facilitate assessment on an individual level does require that individual signals be distinct in some respects.

The results of this section's analyses reveal that the potential for individual male appraisal based on call distinctiveness is unlikely (Table 3.4). The phenomenon of neighbour-stranger discrimination (*sensu* Falls 1982) relies on the ability of territory owners to distinguish between characteristics of neighbours and other conspecifics. In the example of *P. kochi*, such discrimination could be achieved solely through utilising information contained in the vocalisation. However, since call features are well explained by meteorological and morphological covariation and are not statistically distinguishable, it is unlikely that selection has favoured such a mechanism of discrimination. It is possible that a less elaborate form of vocal class discrimination, for example size-based signalling, exists in the gecko system. In this way, resource-holding potential and fighting asymmetries may be reliably assessed (Hammerstein &

Reichert 1988). In the light of this section's judgement, the vocalisation features upon which such appraisal may be based remains obscure. However, the gecko advertisement call's intensity (SPL) covaries reliably with morphology. In this sense, gecko choruses display obvious parallels with the choruses of anuran amphibians (Arak 1983, Ryan 1985) and avian acoustical displays (Loffredo & Borgia 1986). Experimental work has also revealed how males use call intensity as a proximate cue in maintaining spatial organisation within choruses (Section 2). It appears ambiguous whether any other additional information, besides that already manifest in sound intensity, could be used as an assessment signal. However, this assertion remains to be empirically tested.

Behavioural observations suggest that the call of *P. kochi* has a function in mate attraction, and females may use cues associated with these calls in mate choice (e.g. Arak 1983, Ryan 1985, Dyson *et al.* 1992). The hypothesis that females display differential preferences for specific call features of certain males is reliant on evidence that shows that variance for these features exists at the population level (Lande 1987). The majority of the variation associated with call descriptors is seen to be dependent on ambient conditions. However, there remains several identifiable sources of information (assuming, of course, that all sources of information have been correctly identified) that females exercising active choice (*sensu* Arak 1988) may rely upon. First, sound pressure level has been shown to differ significantly between males (Section 2). Second, the spectral sensitivity of the gekkonid ear is well accepted (Sakaluk & Belwood 1984, Manley 1990) and frequency information (AFREQ) contained in male calls has been identified as the principal basis of statistical discrimination between males (Table 3.8). Lastly, there is information contained in call rate (BCI) that is unexplained by the morphological or meteorological covariation examined here (Section 3.2.3). The next section (Sexual selection) is aimed at testing the credibility of these hypothesis for potential sources of information in the vocalisation of *P. kochi*.

Table 3.1 A review of the literature on analytical aspects of vocal communication

Species	Signal Function	Statistical Analysis ^a Approach ^c	Test(s)	Signature ^b invocation?	Source
Sandwich tern <i>Sterna sandvicensis</i>	Parent-offspring recognition	Univariate	Correlation CV	?	Hutchinson <i>et al.</i> 1968
Gannett <i>Sula bassana</i>	Individual recognition in monogamous pairs	Univariate	Correlation	?	White & White 1970 White <i>et al.</i> 1970
American goldfinch <i>Carduelis tristis</i>	Individual mate-recognition	Visual inspection of sonagram		?	Mundinger 1970
Chimpanzee <i>Pan troglodytes</i>	Individual identification	Descriptive statistics ^d		?	Marler & Hobbet 1975
Mangabey <i>Cercocebus albigena</i>	Individual recognition	Descriptive statistics		?	Waser 1977
Manx shearwater <i>Puffinus puffinus</i>	Individual recognition in monogamous pairs and burrow location cue	Visual inspection of spectrograms		?	Brooke 1978

Red Jungle fowl <i>Gallus gallus</i>	Individual distinctiveness	Univariate	ANOVA	?	Miller 1978
Humpback whale <i>Megaptera novaeangliae</i>	Signature information	Univariate/ Multivariate	CV, MANOVA Stepwise DFA	Yes	Hafner <i>et al.</i> 1979
Squirrel monkey <i>Saimiri sciureus</i>	Group member location	Multivariate	MDS, DFA Cluster analysis	Yes	Symmes <i>et al.</i> 1979 Lieblich <i>et al.</i> 1980
Pygmy marmoset <i>Cebuella pygmaea</i>	Individual recognition	Univariate	ANOVA MULT	?	Snowdon & Cleveland 1980
Pinon jay <i>Gymnorhinus cyanocephalus</i>	Parent-young vocal recognition	Univariate/ Multivariate	ANOVA, PCA	Yes	McArthur 1982
Pika <i>Ochotona princeps</i>	Individual recognition	Multivariate	DFA	?	Conner 1985a
Bank swallow <i>Riparia riparia</i>	Individual recognition of parental call by chicks	Univariate	ANOVA	Yes	Sieber 1985
Mexican free-tailed bat <i>Tadarida brasiliensis</i>	Parental recognition of pups	Univariate/ Multivariate	REG ANOVA, DFA	Yes	Gelfand & McCracken 1986
Raccoon <i>Procyon lotor</i>	Mother-cub recognition	Univariate	MW	?	Sieber 1986

Crested tern <i>Sterna bergii</i>	Individual recognition	Univariate	Kruskal-Wallis	?	Veen 1986
Ancient murrelet <i>Synthliboramphus antiquus</i>	Family group cohesion within colonies	Multivariate	MDS, PCA	Yes	Jones <i>et al.</i> 1987
Wilson's storm-petrel <i>Oceanites oceanicus</i>	Individual stereotypy	Univariate	CV	?	Bretagnolle 1989
Lesser spear-nosed bat <i>Phyllostomus discolor</i>	maternal distinctiveness in mother-infant communication	Univariate	ANOVA	Yes	Esser & Schmidt 1989
Leach's storm-petrel <i>Oceanodroma leucorhoa</i>	Vocal sex recognition	Univariate	CV, KS, MW	?	Taoka <i>et al.</i> 1989
Pipits <i>Anthus spinoletta petrosus</i> <i>A. pratensis</i>	Individual recognition	Univariate	ANOVA CV, KS Contingency-table analysis, t-tests	?	Elfström 1990
Pigtail macaques <i>Macaca nemestrina</i>	Matrilineal signatures	Univariate/ Multivariate	ANOVA log-likelihood ratio MULT, DFA	Yes	Gouzoules & Gouzoules 1990
Timber wolf <i>Canis lupus</i>	Vocal signatures	Multivariate	PCA, DFA	Yes	Tooze <i>et al.</i> 1990

Great tit <i>Parus major</i>	Individual identification	Univariate/ Multivariate	ANOVA DFA	Yes	Weary <i>et al.</i> 1990
Tawny owl <i>Strix aluco</i>	Individual recognition	Visual inspection/ Univariate/ Multivariate	CV, ANOVA DFA	?	Galeotta & Paven 1991
A pipistrelle bat <i>Pipistrellus pipistrellus</i>	Individual vocal signature development	Multivariate	DFA	Yes	Jones <i>et al.</i> 1991
Short-toed treecreeper <i>Certhia brachydactyla</i>	Individual distinctiveness	Multivariate	DFA	?	Bauer & Nagl 1992
European starling <i>Sturnus vulgaris</i>	Individual recognition of nestling distress screams	Multivariate	MANOVA	?	Chaiken 1992
Bittern <i>Botaurus stellaris</i>	Individual distinctiveness	Univariate/ Multivariate	ANOVA, DFA	?	McGregor & Byle 1992
Emperor penguin <i>Aptenodytes forsteri</i>	Individual recognition	Univariate/ Multivariate	CV, ANOVA Kruskal-Wallis, DFA	?	Robisson <i>et al.</i> 1993
Evening bat <i>Nycticeius humeralis</i>	Heritable signatures	Univariate/ Multivariate ^f	REG MANOVA, DFA	Yes	Scherrer & Wilkinson 1993

Madagascar hissing cockroach <i>Gromphadorhina</i> <i>portentosa</i>	Social communication	Univariate	ANOVA	?	Clark & Moore 1995
Barbary macaques <i>Macaca sylvanus</i>	Individual differences	Multivariate	Cluster analysis DFA	?	Hammerschmidt & Todt 1995
European bee-eater <i>Merops apiaster</i>	Individual identification of parents by chicks	Multivariate	Cross correlations	?	Lessells <i>et al.</i> 1995
Big brown bat <i>Eptesicus fuscus</i>	Individual identification	Univariate/ Multivariate	Randomisation tests Cross correlations ANOVA, MANOVA Factor Analysis, DFA	Yes	Masters <i>et al.</i> 1995
Bats <i>Euderma maculatum</i> <i>Eptesicus fuscus</i> <i>Lasiurus borealis</i> <i>L. cinereus</i>	Echolocation	Univariate/ Multivariate	CV, MANOVA DFA, MDS	?	Obrist 1995
Bottlenose dolphin <i>Tursiops truncatus</i>	Sex-differences	Human evaluation of spectrograms	?		Sayigh <i>et al.</i> 1995

a	-	For the purposes of this review, multivariate techniques are those that simultaneously consider the variation in several characters. These include Cluster analysis, Multidimensional scaling, Multivariate Analysis of Variance (MANOVA) and all ordination techniques.
b	-	Instances where the word 'signature' is explicitly used in text.
c	-	Levels of approach range from simple visual inspection of vocalisations, descriptive statistical evaluation, univariate hypothesis testing, to multivariate pattern recognition techniques. All approaches other than visual inspection of sonagram/spectrogram investigate features of descriptor measures (parameters) of vocalisations (e.g. duration, peak-frequency).
d	-	Descriptive statistics refer to the simple measures of dispersion and variability (i.e. range, mean, standard deviation etc.)
ANOVA	-	Analysis of Variance (no distinction is made here between nested, hierarchical and general multifactorial designs)
CV	-	Coefficient of Variation
DFA	-	Discriminant Function Analysis
REG	-	Regression analysis
KS	-	Kolmogorov-Smirnov test
MDS	-	Multidimensional Scaling
MULT	-	Multiple comparison tests
MW	-	Mann-whitney U test
PCA	-	Principal Component Analysis

Table 3.2 A review of the literature on experimental^a aspects of vocal communication

Species	Signal Function	Signature invocation?	Source
Ovenbird <i>Sciurus aurocapillus</i>	Neighbour discrimination	?	Weeden & Falls 1959
Laughing gull <i>Larus atricilla</i>	Individual recognition of parents by chicks	?	Beer 1969, 1979
American goldfinch <i>Carduelis tristis</i>	Individual mate-recognition	?	Mundinger 1970
Common tern <i>Sterna hirundo</i>	Individual recognition of parents by young	?	Stevenson <i>et al.</i> 1970
Indigo bunting <i>Passerina cyanea</i>	Neighbour-stranger discrimination	?	Emlen 1971
Reindeer <i>Rangifer tarandus</i>	Individual recognition in mother-young relationships	?	Epsmark 1971
Field sparrow <i>Spizella pusilla</i>	Neighbour discrimination	?	Goldman 1973

Northern elephant seal <i>Mirounga angustirostris</i>	Maternal protection of pups	?	Petrinovich 1974
White-throated sparrow <i>Zonotricha albicollis</i>	Neighbour discrimination	?	Brooks & Falls 1975 Falls & Brooks 1975
Song sparrow <i>Melospiza melodia</i>	Neighbour discrimination	?	Harris & Lemon 1976 Kroodtsma 1976
	Recognition of individual neighbours	?	Stoddard <i>et al.</i> 1991
	Song matching	?	Nielsen & Vehrencamp 1995
Lamb	Hearing recognition of lamb by mother	?	Poindron & Carrick 1976
Mangabey <i>Cercocebus albigena</i>	Individual recognition	?	Waser 1977
Manx shearwater <i>Puffinus puffinus</i>	Individual recognition in monogamous pairs and burrow location cue	?	Brooke 1978
Yellowthroat <i>Geothlypis trichas</i>	Neighbour and mate-recognition	?	Wunderle 1978
Blue grouse <i>Dendragapus obscurus</i>	Male neighbour-stranger discrimination	?	Falls & McNicholl 1979
Rufous-sided towhee <i>Papilo erythrophthalmus</i>	Neighbour discrimination	?	Richards 1979

Vervet monkey <i>Cercopithecus aethiops</i>	Protective vocalisations of mother to offspring	?	Cheney & Seyfarth 1980
Chaffinch <i>Fringilla coelebs</i>	Neighbour discrimination	?	Pickstock & Krebs 1980
Pygmy marmoset <i>Cebuella pygmaea</i>	Individual recognition	?	Snowdon & Cleveland 1980
White-crowned sparrow <i>Zonotrichia leucophrys</i>	Neighbour discrimination	?	Baker <i>et al.</i> 1981
Meadowlarks <i>Sturnella magna</i> , <i>S. neglecta</i>	Neighbour-stranger discrimination	?	Falls & D'Agincourt 1981
Swamp sparrow <i>Melospiza georgiana</i>	Neighbour discrimination	?	Searcy <i>et al.</i> 1982
Pinon jay <i>Gymnorhinus cyanocephalus</i>	Parent-young vocal recognition	Yes	McArthur 1982
Cliff swallow <i>Hirundo pyrrhonota</i>	Individual recognition of parental voice by young	Yes	Beecher <i>et al.</i> 1985
Pika <i>Ochotona princeps</i>	Individual recognition	?	Conner 1985b

Coral reef-fish <i>Pomocentrus partitus</i>	Individual recognition	?	Myrberg & Riggio 1985
Bank swallow <i>Riparia riparia</i>	Individual recognition of parental calls by chicks	Yes	Sieber 1985
Japanese macaques <i>Macaca fuscata</i>	Individual recognition of juveniles by mother	?	Pereira 1986
Raccoon <i>Procyon lotor</i>	Mother-cub recognition	?	Sieber 1986
North American bullfrog <i>Rana catesbeiana</i>	Neighbour recognition	?	Davis 1987
Ancient murrelet <i>Synthliboramphus antiquus</i>	Family group cohesion within colonies	Yes	Jones <i>et al.</i> 1987
Wilson's storm-petrel <i>Oceanites oceanicus</i>	Individual stereotypy	?	Bretagnolle 1989
Leach's storm-petrel <i>Oceanodroma leucorhoa</i>	Vocal sex recognition	?	Taoka <i>et al.</i> 1989
Mexican free-tailed bats <i>Tadarida brasiliensis</i>	Vocal recognition of pups by mother	?	Balcombe 1990

Pipits <i>Anthus spinoletta petrosus</i> <i>A. pratensis</i>	Neighbour-stranger discrimination	?	Elfström 1990
European robin <i>Erithacus rubecula</i>	Neighbour-stranger discrimination Neighbour-neighbour discrimination	?	Brindley 1991
Hooded warbler <i>Wilsonia citrina</i>	Neighbour recognition	?	Godard 1991
European starling <i>Sturnus vulgaris</i>	Individual recognition of nestling distress screams	?	Chaiken 1992
Baboon <i>Papio cynocephalus ursinus</i>	Opponent reconciliation	?	Cheney <i>et al.</i> 1995
Wood warblers <i>Wilsonia citrina</i> <i>Oporornis formosus</i>	Individual recognition of song repertoires	?	Godard & Wiley 1995

a - All literature cited refers to playback experiments

Table 3.3 Predictor variables and abbreviations (underlined) used in the GLM analyses of the barking gecko.

Meteorological Variables	units	Morphological Variables	units
1) dry-bulb temperature at 14h00 hours (<u>DB2</u>)	° C	1) Mass (<u>Mass</u>)	g
2) dry-bulb temperature at 20h00 hours (<u>DB8</u>)	° C	2) Extent of yellow colouration (<u>Yellow</u>)	mm
3) soil-temperature at 5 cm below the sand surface (20h00 hours) (<u>ST5</u>)	° C	3) Sound pressure level (<u>SPL</u>)	dB
4) soil-temperature at 10 cm below the sand surface (20h00 hours). (<u>ST1</u>)	° C	4) Snout-tail length (<u>Length</u>)	mm
5) soil-temperature at 20 cm below the sand surface (20h00 hours). (<u>ST2</u>)	° C		
6) soil-temperature at 30 cm below the sand surface (20h00 hours). (<u>ST3</u>)	° C		
7) Ambient temperature upon calling (<u>AT</u>)	° C		
8) Night minimum temperature (<u>MIN</u>)	° C		
9) Relative Humidity (20h00 hours) (<u>RH</u>)	%		
10) Windspeed (20h00 hours) (<u>WS</u>)	m/sec		

Table 3.4 Barking gecko GLM Summary: dependent variables, the model's selection of independent variables (and all significant interactions), probability-values and the adjusted R^2 values are presented. The descriptor measures were first adjusted for morphological covariation (adjustment for morphological variability) and then the residual matrix from this procedure was used in adjusting for meteorological covariation (adjustment for meteorological variability).

Dependent variable	Selected Independent variables	P-value of GLM	Adjusted R^2
<u>Adjustment for morphological variability</u>			
BCI	Mass	0.000	0.070
DOC	Mass; Length; SPL; Yellow*Length	0.000	0.203
RANGE	Length; Mass*Yellow*Length; Yellow*Length*SPL	0.000	0.259
AFREQ	Length; SPL; Mass*Yellow; Yellow*Length*SPL	0.000	0.159
<u>Adjustment for meteorological variability</u>			
BCI	AT; ST5; AT*ST5	0.003	0.073
DOC	AT; ST1; MIN; RH*ST3*WS*MIN; AT*RH*T5; AT*ST1*WS AT*ST5; ST5*WS	0.000	0.722
RANGE	RH; ST1; AT*ST1 RH*ST5*WS*MIN; AT*ST5*WS; AT*RH*ST1	0.000	0.222
AFREQ	AT; RH; ST5; ST5*RH*MIN; ST5*WS*MIN; AT*RH*ST1 AT*RH*WS AT*ST1; ST1*WS	0.000	0.500

Table 3.5 The summary of discriminant function analysis results for the soft-chirp of the naked mole-rats. Eigenvalues, relative percentage variance explained, Wilks' lambda, Chi-square, canonical correlation coefficients, degrees of freedom (df) and probability level (p-level) statistics are presented. Discriminant functions with eigenvalues less than one have been excluded from the analysis at this stage. The results from the analysis on the original soft-chirp descriptor measures (unadjusted) and those first regressed on body-mass (adjusted for morphological covariation) are presented here.

Discriminant		Relative	Wilks'	Chi-	canonical	(df)
Function	Eigenvalue	percentage	lambda	square	correlation	p-level
<u>Unadjusted</u>						
1	19.28	63.63	0.0006	2306.48	0.975	(80) 0.000
2	5.86	19.49	0.0126	1366.03	0.924	(63) 0.000
3	1.51	7.18	0.0867	764.05	0.776	(48) 0.000
4	1.00	5.24	0.2177	476.40	0.707	(35) 0.000
<u>Adjusted for morphological covariation</u>						
1	11.53	63.67	0.0020	1940.13	0.959	(80) 0.000
2	3.60	23.35	0.0252	1150.04	0.884	(63) 0.000
3	1.25	5.47	0.1158	673.85	0.745	(48) 0.000

Table 3.6 Standardised coefficients for canonical variables and their associated factor loadings for the discriminant function analyses of the soft-chirp of the naked mole-rat. Unadjusted and adjusted canonical coefficients are presented. Underlined characters indicate those variables that load conspicuously within any one canonical function.

Variable	Function 1	Function 2	Function 3	Function 4
----------	------------	------------	------------	------------

Unadjusted

DUR	0.1457	<u>1.3933</u>	<u>2.6198</u>	<u>2.3581</u>
TTP	0.1637	- <u>0.9995</u>	- <u>2.4019</u>	- <u>3.5822</u>
RPP	0.3602	<u>1.5507</u>	<u>2.0799</u>	<u>2.9079</u>
PKFQ	- <u>1.7351</u>	0.7022	0.3661	- 0.0777
FQR	<u>1.1234</u>	- <u>1.4456</u>	- 0.5399	- 0.0344
SS	- 0.3077	- 0.5752	- 0.4255	- 0.2106
DS	0.4989	- 0.0094	0.4721	- 0.1256
RELXY	- 0.1115	- 0.2895	0.4215	0.6088

Adjusted for morphological covariation

DUR	- 0.1376	- <u>0.7058</u>	<u>0.7496</u>
TTP	0.2349	0.3243	- 0.2237
RPP	- 0.0885	- 0.5860	0.0238
PKFQ	- <u>1.7837</u>	- 0.0804	0.4195
FQR	<u>1.4226</u>	<u>1.0418</u>	- <u>0.8469</u>
SS	- 0.0292	0.1812	- 0.1435
DS	0.4438	- 0.0127	0.3716
RELXY	- 0.0367	0.5778	0.1460

Table 3.7 The summary of discriminant function analysis results for the advertisement bark of the barking gecko. Eigenvalues, relative percentage variance explained, Wilks' lambda, Chi-square, canonical correlation coefficients, degrees of freedom (df) and probability level (p-level) statistics are presented. Discriminant functions with eigenvalues less than one have been excluded from the analysis at this stage. The results from the analysis on the bark descriptor measures (unadjusted), those first corrected for morphological covariation (adjusted for morphological covariation), and those corrected for the combined influence of both morphological and meteorological covariation (adjusted for both morphological and meteorological covariation) are presented here.

Discriminant		Relative	Wilks'	Chi-	canonical	(df)
Function	Eigenvalue	percentage	lambda	square	correlation	p-level
<u>Unadjusted</u>						
1	11.92	66.66	0.0062	1472.26	0.961	(56) 0.000
2	4.81	26.93	0.0799	731.42	0.910	(39) 0.000
3	1.14	6.40	0.4650	221.68	0.731	(24) 0.000
<u>Adjusted for morphological covariation</u>						
1	9.62	68.43	0.0124	1271.42	0.952	(56) 0.000
2	3.88	27.62	0.1315	587.32	0.892	(39) 0.000
<u>Adjusted for both morphological and meteorological covariation</u>						
1	1.04	62.12	0.2847	363.67	0.715	(56) 0.000

Table 3.8 Standardised coefficients for canonical variables and their associated factor loadings for the discriminant function analyses of the advertisement bark of the barking gecko.

Unadjusted, and canonical coefficients adjusted for morphological covariation, and those corrected for the combined influence of both morphological and meteorological covariation are presented. Underlined characters indicate those variables that load conspicuously within any one canonical function.

Variable	Function 1	Function 2	Function 3
----------	------------	------------	------------

Unadjusted

BCI	0.0339	- 0.1490	- 0.0213
DOC	0.0649	<u>1.0401</u>	- 0.0550
RANGE	- 0.2650	- 0.0615	- <u>0.9687</u>
AFREQ	<u>1.009</u>	0.2023	- 0.1693

Adjusted for morphological covariation

BCI	0.0079	- 0.1484
DOC	0.2479	<u>0.9944</u>
RANGE	- 0.1712	- 0.1801
AFREQ	<u>1.041</u>	0.0151

Adjusted for both morphological and meteorological covariation

BCI	0.1815
DOC	- 0.1412
RANGE	- 0.0147
AFREQ	<u>0.9790</u>

Table 3.9 Summary of the forward stepwise-regression : (a) initial predictor variables, (b) predictor variables selected by the best subset model, and (c) multiple-regression summary

(a) INITIAL PREDICTOR VARIABLES

14h00 temperature	soil temperature at 20 cm
20h00 temperature	temperature difference
effective moonlight	temperature decay range
relative humidity	time
soil temperature at 5 cm	windspeed
soil temperature at 10 cm	

(b) THE SUBSET MODEL INCLUDES THE FOLLOWING PREDICTORS:

Constant	Soil temperature at 20 cm
20h00 temperature	Time
Relative humidity	Temperature difference
Windspeed	

(c) MULTIPLE-REGRESSION RESULTS

DEPENDENT VARIABLE: CHORUS DURATION

N: 63

ADJUSTED SQUARED MULTIPLE R: 0.776

STANDARD ERROR OF ESTIMATE: 7.324

VARIABLE	COEFFICIENT	STD ERROR	T-stat	P(2 TAIL)
Constant	10.525	24.728	-0.426	0.673
20h00-temp	.137	0.814	6.308	0.000
Rel-humidity	0.459	0.154	2.971	0.005
Windspeed	1.785	0.714	-2.499	0.017
Soil-temp-20cm	-1.575	0.885	-1.780	0.044
Time	0.433	0.103	-4.187	0.000
Temp-diff	5.146	1.167	-4.411	0.000

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	4911.744	6	818.624	15.260	0.000
RESIDUAL	1931.232	56	53.645		

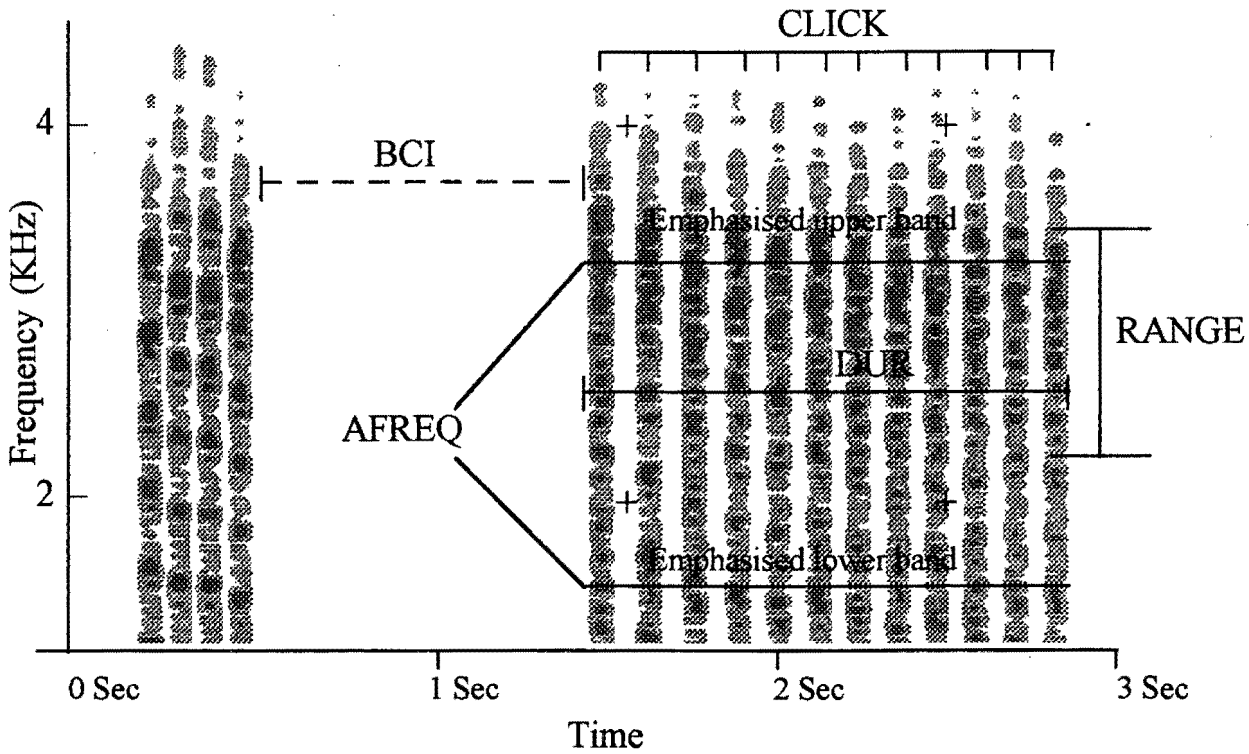


Fig. 3.1 A representative gecko 'bark' sonagram. Measured features of the call are indicated: BCI (between-call interval), DUR (duration), CLICK (total number of clicks in any one call), RANGE (frequency range of the broader emphasised harmonic) and AFREQ (average frequency).

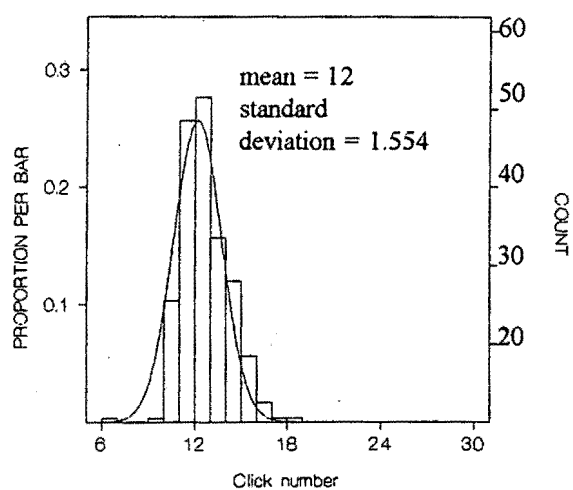


Fig. 3.2 A histogram displaying the frequency distribution of click number of a sample of 300 *P. kochi* calls. Summary statistics (mean and standard deviation) are indicated. A normal distribution curve is fitted to the observed distribution.

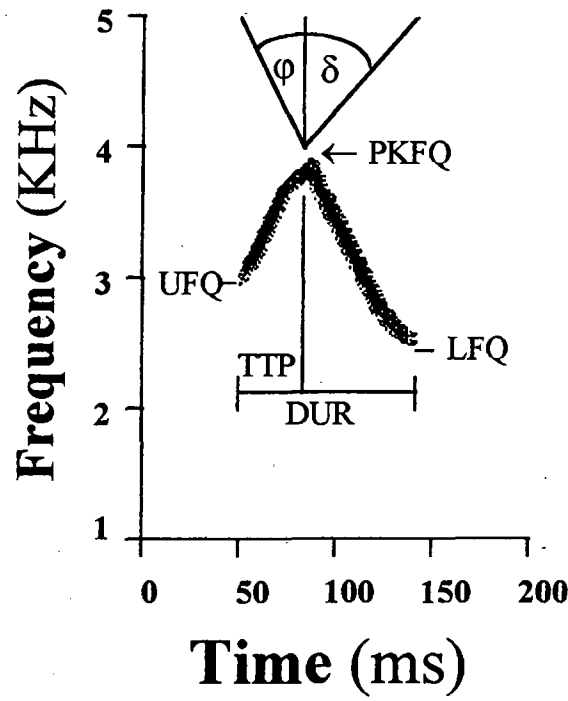


Fig. 3.3 A representative soft-chirp sonagram. Measured features of the call are indicated: DUR (duration), TTP (time to peak), UFQ (upper frequency), LFQ (lower frequency), PKFQ (peak frequency), ϕ (angle of downslope) and δ (angle of upslope).

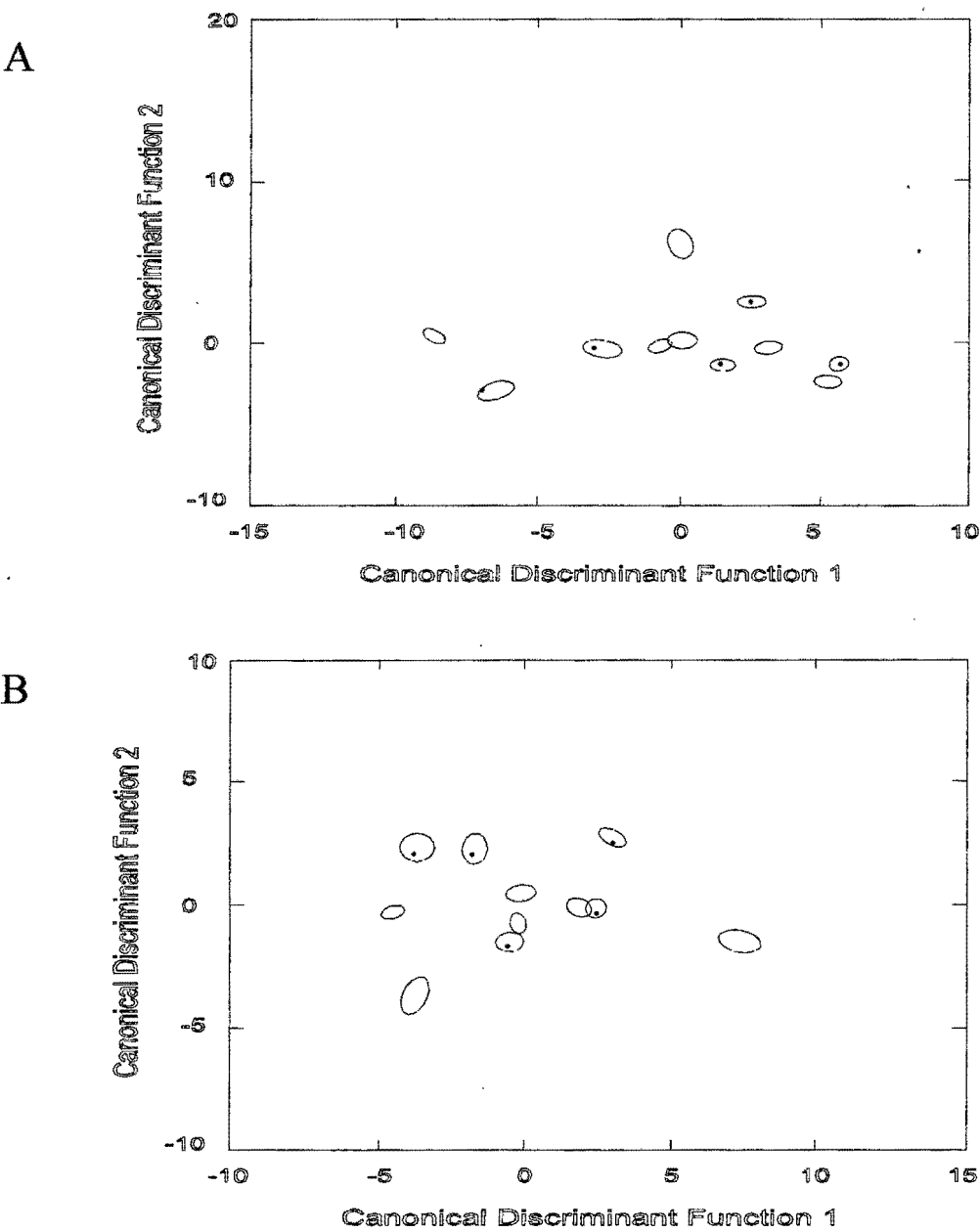


Fig. 3.4 A plot of 95% bivariate centroids for each repeated-measure group of 11 individuals naked mole-rats in discriminant signal space for the first two canonical discriminant functions. The centroids of only the male naked mole-rats are indicated; A) Unadjusted for individual descriptor measure scores, B) Adjusted for covariation of descriptor measures with mass.

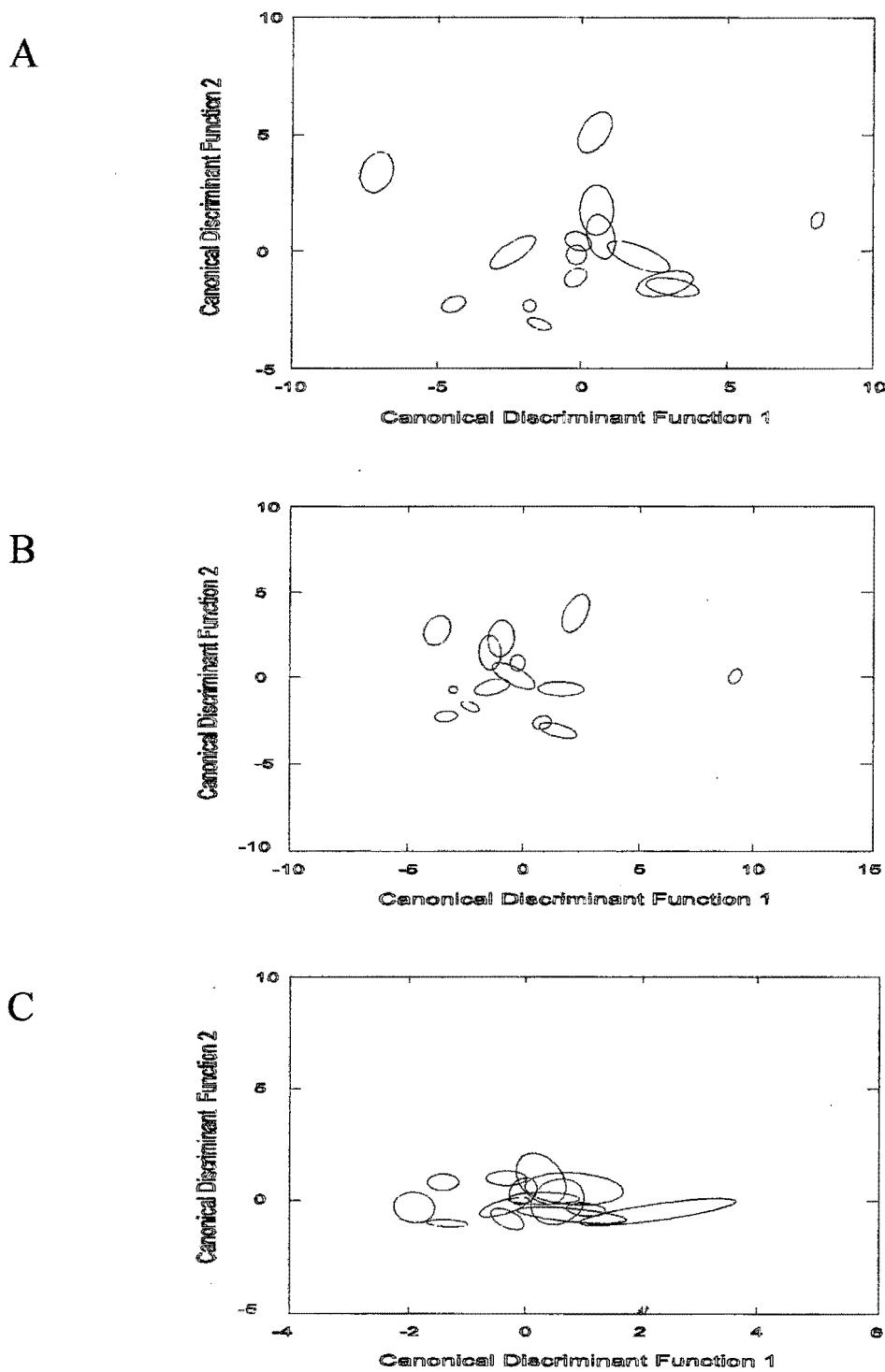


Fig. 3.5 A plot of 95% bivariate centroids for each repeated-measure group of 15 individual barking geckos in discriminant signal space for the first two canonical discriminant functions; A) Unadjusted for individual descriptor measure scores, B) Adjusted for morphological covariation, C) Adjusted for morphological and meteorological covariation

SECTION 4

Sexual selection

The theory of sexual selection was proposed by Charles Darwin as a means of explaining the existence of elaborate male structures and behaviour patterns that seemed to be at odds with an individual's survival. Darwin (1871: p. 256) defined sexual selection as "the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction". According to Darwin, sexual selection is evidenced in two distinct forms - competition within a sex for access to members of the opposite sex (intrasexual selection), and selection driven by the choice by individuals of one sex (usually females) for particular members of the opposite sex (intersexual selection). This classification is often seen to fail, however, as characters used in male-male competition often play a role in female choice (e.g's Von Schantz *et al.* 1989, Harvey & Bradbury 1991). Understanding the relative contribution of intrasexual competition and intersexual choice components in mating systems remains an obscure and controversial issue (Bradbury & Davies 1987, Andersson 1994).

This section is an attempt to explore the potential of mate selection acting in the mating system of *P. kochi*. First, mate choice is defined and current theory on the two 'indirect' models of sexual selection are reviewed. Second, predictions about female mate choice for male characteristics are discussed and the objectives of this section noted (Section 4.1).

Third, correlates of female mate choice are presented (Section 4.2). Lastly, the results from the findings on sexual selection in *P. kochi* are discussed (Section 4.3).

Mate-choice

Before discussing theories attempting to explain the evolution of mate preference, it is necessary to first define mate choice and to be aware of the difficulties involved in its empirical verification. Mate choice may be defined as any pattern of behaviour, shown by members of one sex, leading to their being more likely to mate with certain members of the opposite sex than with others (Halliday 1983). This operational definition obviates the requirement for understanding the neural mechanism(s) involved in the selective responsiveness of animals to particular stimuli. It is also broad enough to encompass what Parker (1983) has termed 'passive' mate attraction and 'active' mate choice. Passive attraction is thought to occur when a prospecting mate simply approaches a signal that best stimulates its nervous system. Conversely, active mate choice is used to describe the patterning of preference evidenced when 'obvious' mate sampling behaviour occurs.

Sexual selection & Natural selection

The relationship between the theories of sexual selection and natural selection is one of the most debated subjects in evolutionary biology today (see Mayr 1972, Halliday 1983, 1992, Arnold 1983, Endler 1986). There has been a resurgence of interest in sexual selection over the last several decades, particularly in theories attempting to account for the intersexual component of animal behaviour. The adaptive significance of mate preference and the potential mechanisms of mate choice remain a predominant focus of much research (Bateson 1983, Pomiankowski 1988, Harvey & Bradbury 1991, Kirkpatrick & Ryan 1991, Ryan & Keddy-Hector 1992, Andersson 1994, Møller 1994, Johnstone 1995).

There is now strong empirical evidence confirming the importance of female choice leading to the evolution of male secondary sexual (epigamic) traits (reviewed in Møller 1994). The evolution of adaptive female choice is not in doubt for species in which males provide females with resources or parental care, as female choice will have clear and direct consequences for fitness (Kirkpatrick 1985). Researchers of sexual selection have,

however, tended to hold divergent views about the role of female choice and its evolutionary consequences in isolation from the presence of male resources.

Historically, there have been two principal models that aim to explain the evolution of female choice by indirect (genetic) selection - the 'Fisherian' and 'handicap' models. Fisherian sexual selection theory predicts that female preference for particular male phenotypes will lead to the evolution of increased expression (runaway) of the traits until sexual selection is balanced by opposing selection pressures (Fisher 1930, Lande 1981, Kirkpatrick 1982). Conversely, handicap models of sexual selection suggest that males develop secondary sexual characters to a level where the increased mating advantage for a male of any given quality is balanced against the cost of acquiring an even larger handicap (Zahavi 1975, Grafen 1990, Iwasa *et al.* 1991). Selective females gain fitness advantages for their offspring by mating with quality males as their offspring inherit general viability benefits. There has been much debate about whether epigamic traits evolve arbitrarily because of linkage disequilibrium caused by the presence of a genetic correlation between the male trait and female preference for the trait (the Fisherian model) (O'Donald 1980, Lande 1981, Kirkpatrick & Ryan 1991), or whether sexually selected traits evolve by indicating the genetic quality of the males bearing them (the handicap model) (Zahavi 1977, Andersson 1982, Pomiankowski 1987, Grafen 1990).

The handicap model predicts that the level of expression of a male ornament is an honest indicator of genetic quality - higher quality males are better able to cope with the expression of costly signals. Such signals should be reliable indicators of features such as age, dominance, parasite load or vigour in males (Andersson 1982, 1986, Hamilton & Zuk 1982, Kodrick-Brown & Brown 1984, Nur & Hasson 1984, Pomiankowski 1987). Females should prefer males reflecting such attributes, and females should use male indicators that honestly reflect these qualities during mate choice. The key to elucidating the selection pressures that limit the expression of sexually selected traits would seem to lie in understanding the costs of male displays (Sutherland & De Jong 1991).

The finding that characters used by females in mate selection often involve severe costs has been used as evidence that such characters are not arbitrary but are indicators of 'good

genes'. The observation that sexually selected traits are costly is, however, compatible with both hypotheses for the evolution of male secondary sexual characters for several reasons. These include the understanding that the outcome of a Fisherian runaway process will be halted when preferred traits become costly to produce, and only relatively viable males will be able to develop them fully (Balmford & Read 1991, Jennions 1993, Backwell *et al.* 1995). Both Fisherian and handicap models predict a positive relationship between trait magnitude and male quality. The endpoint of the Fisherian process is thus also likely to be a costly ornament.

Studies of the current adaptive value of a trait provides limited information about its evolutionary history (Williams 1966, Gould & Vrba 1982). Since both Fisherian and handicap models predict the same possible outcome of costly ornamentation, extreme caution should be exercised before concluding that secondary sexual traits with these properties have evolved because they signal male quality. However, an argument presented recently by Reeve & Sherman (1993) provides a distinction that is useful here. They maintain that adaptations can be understood either by an account of their selective history, or by investigating why a trait is maintained in the population at present. Only the assumption that all traits conferring selective advantages have evolved for their present function justifies a study determining evolutionary history from current selective value. This line of reasoning is not often justified and the present maintenance of sexually selected traits is clearly still open to investigation. In this research, the current maintenance value of male *P. kochi* behaviour is studied.

Patterns of mating among *P. kochi* individuals appears to be polygynous. Males are territorial, and defend small exclusive acoustic spaces that are spatially distinct from females. Females sample several males before selecting a mate, and long-term associations in a chosen male's burrow appear to be commonplace (see Section 1.5). Eggs are laid in male burrows, and newly hatched juvenile geckos occupy their father's burrows for the first few weeks of their lives before dispersing (Section 1). Males may thus contribute indirectly to parental care, as well as providing suitable oviposition sites for females. There may also be other unconsidered advantages to females residing in male burrows (e.g. predator avoidance). In the presence of obvious male resources, any benefits to females of mate

choice based on aspects of male quality might be indirect and potentially outweighed by the direct benefits of choice for a male resource (Howard 1978, Halliday 1983). Female behaviour is expected to be far more subtle compared to conspicuous male territorial activities.

Understanding the relative importance of female choice for male traits and choice for defended resources is inherently difficult, since male phenotypic characteristics are likely to be confounded with aspects of territory quality (Howard 1978, Catchpole *et al.* 1985). However, several studies in birds and fish have managed to document the independent effects of territory quality (Ewald & Rohwer 1982) or male parental ability (Downhower & Brown 1980, Simmons 1988). Both male and resource quality have also been suggested to be important in polygynous fish (Thomson 1986) and bird species (Alatalo *et al.* 1986, 1990, Reid & Weatherhead 1990).

The evolutionary significance of any form of sexual selection must be the extent to which genetic variation in males and females covaries with fitness. If pure male-male competition is simply a theoretical construct, then there should be no genetic variation in females with the fitness of their mating partner(s). Conversely, if covariance does exist, then there will be the evolution of female mate preferences. The degree to which mate choice by females occurs in systems where male-male competition predominates will depend largely on the extent to which females show a 'consensus' in terms of their choice of males (Halliday 1983). Congruence between the observed patterns of female mate selection in *P. kochi* and several aspects of male vocal and territorial behaviour were studied in an attempt to understand the potential for the evolution of female mate preference in the barking gecko system.

4.1 Objectives and Methods

Predictions about mate choice ?

Assuming that mate choice for male traits is occurring in *P. kochi*, which features are expected to be preferred by females? Handicap theory predicts that only costly traits can act as honest signals (Grafen 1990, Zahavi 1993). Intuitively, a negative relationship is expected between traits that are energetically expensive and the level of expression of that trait (e.g. call intensity and call repetition rate). A sexually selected trait should display condition dependence - where high quality males are likely to be in better condition and should invest more heavily in sexually selected characters. A positive correlation between body condition, and the level of expression of a sexually selected trait is predicted for a trait that is condition-dependent (Alatalo *et al.* 1991, Hill 1991, Møller 1994).

Phenotypic correlates

Phenotypic characteristics of males or features of burrow quality might be involved in mate selection once a female approaches a prospective male, and enters into his burrow system. Body size in male lizards is known to be a good indicator of fitness in terms of natural selection. Body size is generally correlated with age, and should therefore indicate survivorship (Halliday & Verrell 1988, Halliday 1992). Body size may represent past or current growth rate, the ability to forage, and is also known to be highly correlated with dominance in male-male aggressive interactions in several lizard species (Ruby 1984, Andrews 1985, Tokarz 1985). Body size is also the most common correlate of resource holding potential (RHP, Parker 1984). However, other factors such as body condition (Thornhill & Sauer 1992), residency status (Rosenberg & Enquist 1991, Olsson 1992, Turner 1994), or the perceived value of a resource (reviewed in Keeley & Grant 1993) are also known to influence contest success.

Methods used for quantifying phenotypic measures (including yellow colouration and sound pressure level (SPL)) are described in Section 1.3. SPL was shown to differ between males and to be significantly related to mass, length and extent of yellow gular colouration

(Section 1.5). However, SPL was seen to be unrelated to both territory size and to residency status (Section 2.3.2). In this section, mass, length, extent of gular yellow colouration and SPL are examined for any differences between mated and non-mated calling males.

Vocalisation correlates

Initial female *P. kochi* mate sampling appears to be based solely on acoustic cues - no other sensory modality is likely to be involved in the process whereby a female leaves her foraging area and enters into the acoustic territories of chorusing males in order to select a mate. The way in which calling behaviour influences mating success has been studied in a number of anuran species (e.g. Gerhardt 1982, Sullivan 1983, Passmore *et al.* 1992, Jennions *et al.* 1995). Several of these studies have focused on the enhanced probability that individual males gain in attracting sexually receptive females by outsignalling (*sensu* Parker 1983) conspecific competitors. Within chorus evenings, a male anuran's vocal behaviour is known to be differentially attractive to females. For example, discrimination experiments have revealed several factors influencing the choice of mates by females, including call complexity (Schwartz 1986, 1987), call persistence (Forester *et al.* 1989), call duration (Doherty & Gerhardt 1984, Klump & Gerhardt 1987), call intensity (Ryan 1985, Schwartz 1986, Arak 1988, Höglund & Robertson 1988, Bishop *et al.* 1995) and call repetition rate (reviewed in Gerhardt 1988, e.g.'s Morris & Yoon 1989, Lopez & Narins 1991, Passmore *et al.* 1992). Female preferences for higher display rates have also been documented in insects and birds (Ryan & Keddy-Hector 1992).

The vocalisation features describing the call of *P. kochi* are noted in Section 3.1. Studies of the patterns of variation in the call descriptors of the advertisement vocalisation of *P. kochi* revealed how most of the variation in the call descriptor DOC (duration/click) is well accounted for by its covariation with meteorological variables (Section 3.3.9). RANGE (frequency range) was seen to covary to a small degree with both morphological and meteorological variability, but it did not explain observed differences between individual calls in discriminant signal space (Section 3.3.9). This patterning of variation in call descriptor measures suggests *a priori* that the information contained in DOC and RANGE are unlikely to be involved in mate selection, should it be occurring.

Female preference for low frequency calls is also known in anurans (Ryan 1983, Nevo & Capranica 1985, Polakow *et al.* 1995). Most often, frequency is negatively correlated with body size (Davies & Halliday 1978, Ryan 1980, Robertson 1986). Researchers have often assumed that larger males are of better quality than smaller males, and that female preference for low frequency calls could be an adaptive trait allowing them to mate with larger males (but see Gerhardt 1988). Frequency information (AFREQ) contained in male *P. kochi* calls was identified as the principal basis of discrimination between males (see Table 3.8) and the spectral sensitivity of the gekkonid ear is well accepted (Sakaluk & Belwood 1984, Manley 1990). AFREQ also covaried significantly with several meteorological variables (Table 3.4) but was not, however, correlated to any substantial degree with any phenotypic traits.

Lastly, little of the variation in call rate (BCI) was suitably explained by morphological or meteorological factors. BCI was seen to decay at significantly different rates between individuals (Section 3.2.3) and to be independent of the effects of temperature. BCI did not feature, however, as a major basis of discrimination between males (Table 3.4), although this cannot preclude the potential for BCI acting as a mating cue. Females responding to males disproportionately producing energetically costly signals may obtain fitness benefits as their male offspring would be more attractive than slower callers. Correlates of call features and mating success are investigated in *P. kochi* in this section.

Residency, burrow activity, and acoustic territory size

Territory size is often a good predictor of mating success (Howard 1978, Arak 1983). Attendance is also known to influence mating success in a number of bird (e.g. Gibson & Bradbury 1985, Andersson 1989) and chorusing anuran species (e.g. Gatz 1981, Arak 1983, Godwin & Roble 1983, Gerhardt *et al.* 1987, Gottlander 1987, Arak 1988, Morris 1989, Rietke & Semlitsch 1991, Dyson *et al.* 1992). In reptiles, residency is also known to be an important determinant of both dominance and mating opportunity (e.g. Niblick *et al.* 1994).

While measures of internal burrow quality were not investigated, the number of burrow entrances a vocal male utilised over his chorus site tenure and a male's activity among his burrows may be considered an index of burrow (territory) size. Methods used for quantifying

burrow activity are described in Section 1.6. Burrowing activities are contrasted between mated and non-mated calling males.

Methods used for quantifying residency (tenure) rankings are described in Section 1.6. The parameter - shared acoustic space ($rx_{(1)}$) - is derived in Section 2.3. The size of shared acoustic space between males showed no obvious relationship to any phenotypic features, but longer burrow tenures were associated with average-sized acoustic territories (Section 2.3.2). Body size has often been indicated as a reliable cue for gauging resource holding potential (RHP, Parker 1974) and contest outcome, since size is naturally related to strength. Agonism of males to the playback speaker during phonotaxis trials showed an interesting association with length of residency, with individuals having spent longer tenures at the chorus site being more likely to engage in aggressive behaviour. However, morphological traits of males showed no relationship to levels of agonism. Data from *P. kochi* suggest that RHP is influenced more by factors relating to the history of male contestants than to morphological correlates. It would be interesting to understand whether historical factors, such as residency, are related to mating success. Correlates of territory size (shared acoustic space) and residency are examined in this section for relationships with mating success.

Energetics of calling?

Research into lekking sage grouse has shown that display performance is correlated with mating success, and that displaying is energetically costly (Bradbury *et al.* 1985, Vehrencamp *et al.* 1989). Other studies of birds show how song rates decrease as thermoregulatory stress increases (Garson & Hunter 1979, Gottlander 1987, Reid 1987) and how song rate increases with food availability (Searcy 1979, Davies & Lundberg 1984, Gottlander 1987, Reid 1987). Since ectotherms have lower metabolic rates, they are expected to show less appreciable energetic constraints than birds (Seale 1987). However, studies of anurans have revealed high energetic costs of male advertisement displays (Taigen & Wells 1985, Robertson 1986, Klump & Gerhardt 1987, Wells & Taigen 1989), and males are known to abandon mating territories after their energetic reserves have been depleted (Wells 1978). The variation manifest in an individual's nightly chorus tenure and activity level on any one night has been related to reduced foraging opportunities experienced by territorial anuran males (Woolbright 1985, Woolbright & Stewart 1987),

and to the high energetic costs of vocalising (Taigen & Wells 1985, Ryan 1985, Wells & Taigen 1986). Work on the reproductive strategies of the teiid lizard *Ameiva plei* documented male mate-guarding, and showed how guarding males spent significantly less time foraging than males who were alone (Censky 1995).

In *P. kochi*, there is substantial variation between males in both chorus site tenure and vocal activity (Section 1 and Section 3). Furthermore, non-caller adult males weigh significantly less than do calling individuals. Data on the mass of eight calling individuals that were marked initially and recaptured some time later (dates of both times noted) are examined. The reduction in body mass is contrasted between captures, and trends in weight loss are investigated for a relationship with time.

Chorus patterning

Lastly, it is possible that competition between males could produce the observed variation in mating success, and that female preference for particular male traits need not be invoked at all. If male *P. kochi* individuals assort themselves with respect to quality through the process of male-male competition, females may accord with the outcome of this process simply because males of the highest quality will get access to females. There might be no reason, therefore, for females to make an active choice of a mating partner if males have resolved in advance all the problems with quality assortment (Møller 1994). This would be the case if females were attracted to a particular location on the chorus site as opposed to a particular male (e.g. Wiley 1974, Borgia 1979). The outcome of such spatial competition would be that males situated in some favoured area of the chorus (most often the centre of display areas) would be more successful than other males (e.g. Bradbury & Gibson 1983, Höglund & Lundberg 1987). It is known that male *P. kochi* individuals in the study site aggregated around a centrally located patch of *Acacia albida* vegetation (Section 1), and that competition for territories occurred within this male aggregation (Section 2). It is possible that females select mates based on proximity to the chorus centre. This hypothesis is tested by looking at whether mated males were significantly closer to the vegetation patch than other non-mated calling males.

Three-dimensional plots and pattern smoothing by the fitting of second-order quadratic equations to data are used to consider the distributions of sound intensity, body mass differences and residency rankings among males on the study site. The spatial distribution of matings among males on the study site area are similarly investigated. The process of recognising chorus patterning using these graphical techniques, although useful, is essentially qualitative.

Statistical analyses

There are many reasons why the identification of mate choice cues is difficult, including the fact that a wide range of potential cues need to be considered simultaneously (e.g. spatial cues within the territorial aggregation, display rate, agonistic status etc.). In order to distinguish reliably between alternatives in a statistical sense, all possible cues of the system need to be quantified and a multivariate statistical technique used to tease apart the independent effects of each factor from the spurious effects due to intercorrelations between the measures (e.g. Lande & Arnold 1983). The difficulty of a single investigator collecting all appropriate data, combined with the low documented rate of matings in the sample *P. kochi* population, implies that such statistical procedures were not possible in this study. Nonparametric inferential statistics are used in testing for significant mating associations. Morphological, call descriptor, burrow, residency and $rx_{(1)}$ measures are tested for significant differences in the distributions of their rankings between males that mated (sample size = 3 males) and those calling males that did not mate (sample size = 12 males). Spearman rank correlation is used to assess the relationship between mass loss and time on the chorus, and between BCI and residency. Differences in BCI between mated and unmated calling males are also investigated using a two-way ANOVA. Bonferroni adjustments are made (where applicable) to probability levels in order to minimise the likelihood of type I errors (the rejection of a true H_0 -hypothesis).

4.2 Correlates of mate choice

Phenotypic correlates of mating success?

Measures of body mass, length, SPL and extent of yellow gular colouration were contrasted between mated and non-mated calling males. No significant differences were found between the two groups in any of these measures (Mann-whitney U : mass : $U = 7$, $n_1=3$, $n_2=12$, $P = 0.77$; length : $U = 0$, $n_1=3$, $n_2=12$, $P = 1.00$; SPL : $U = 0$, $n_1=3$, $n_2=12$, $P = 1.00$; yellow : $U = 3$, $n_1=3$, $n_2=12$, $P = 0.885$).

Call feature correlates of mating success?

Twenty recordings were taken from each of 15 males, and average values for RANGE, AFREQ and BCI obtained for each male. DOC is known to be strongly dependent on temperature and so it was first regressed on temperature (see Section 3.2.5) and then an average taken from the regression residuals for each individual. Differences in values between mating and non-mating males were then tested. No differences between the two classes of males were found in AFREQ, RANGE or DOC (Mann-whitney U tests : AFREQ : $U = 2.4$, $n_1=3$, $n_2=12$, $P = 0.828$, $P_{adj} = 1$; RANGE : $U = 2.4$, $n_1=3$, $n_2=12$, $P = 0.828$, $P_{adj} = 1$; DOC : $U = 2.4$, $n_1=3$, $n_2=12$, $P = 0.828$, $P_{adj} = 1$). However, call rate did differ significantly between the two groups (BCI : $U = 35$, $n_1=3$, $n_2=12$, $P = 0.01$, $P_{adj} = 0.04$).

Averaged values for BCI cannot account for the variation between individuals in call rate. For this reason, the relationship between BCI and mating success was analysed parametrically using an ANOVA incorporating the original 15 x 20 matrix for logBCI (see Section 3.2.3). The presence or absence of mating, and the 30 repeated measures on each individual were used as the two, two and 15 level factors respectively, in an unbalanced two-way ANOVA. The results showed that mating success was a significant factor; mated males called more often than unmated males (Mating success : $F = 15.568$, d.f. = 1,284, $P < 0.001$).

The recording samples used here were taken from individual males over only one night of their calling activity during the study period. It is intriguing to find that these 'snapshot' samples

turned out to be significant predictors of mating status. Observations over the study period suggested that call rate was relatively stable within males, as males calling frequently on any given night clearly tended to do so consistently over their chorus site tenure. The repeatability of within-male call rate is cautiously assumed for this study, but it would be useful to test this in a more rigorous way.

Burrow activity and mating success?

Differences in the burrow activities between mated and unmated males were compared. First, the percentage of time that male's burrow entrances were open was investigated. Mated males showed a significant tendency to have their entrances open a far greater percentage of the time (Mann-whitney U : $U = 35$, $n_1=3$, $n_2=12$, $P = 0.01$, $P_{adj} = 0.03$). Second, the number of weeks that a burrow entrance was active within any one stretch of time (a burrow entrance's 'run') was compared between the two groups of calling males. Mated males' burrows revealed significantly longer runs than unmated males ($U = 38$, $n_1=3$, $n_2=12$, $P = 0.001$, $P_{adj} = 0.003$). Lastly, the number of burrow entrances that each calling male occupied over his tenure at the chorus site was contrasted between the two groups of males. Mated males show a significant tendency to have a larger number of entrances ($U = 35$, $n_1=3$, $n_2=12$, $P = 0.01$, $P_{adj} = 0.03$).

Residency, $rx_{(1)}$ and mating success?

A parabolic relationship between $rx_{(1)}$ and residency was witnessed in Section 2.3.2. This relationship displayed statistical significance when linearised ($rx_{(1)}$ was truncated at its average value and residency scores above this value transformed). More persistent individuals were seen to have average-sized acoustic territories. The relationship between $rx_{(1)}$ and mating success was also seen to be significant once similarly transformed ($r = 0.880$). Here $rx_{(1)}$ was truncated at its average value and the mating status of males above this value were assigned the numeral 2 (0 and 1 being the states before truncation). Mated males were seen to have average-sized acoustic territories.

Residency rankings were compared between mated and non-mated males. Residency differed significantly between the two male groups ($U = 35.5$, $n_1=3$, $n_2=12$, $P = 0.008$, $P_{adj} = 0.024$) with mated males ranking highest on the residency scale, and were clearly the more permanent individuals at the chorus site. Lastly, BCI differed significantly between males of

different residency rankings (Kruskal-Wallis, $n_1 = 4$, $n_2 = 3$, $n_3 = 7$, $K = 6.933$, $P = 0.031$) with more permanent individuals being the more frequent callers ($r = 0.700$).

Is calling energetically expensive?

An analysis of the differences between mass measures on recaptured calling males revealed a significant reduction in body mass between captures (Wilcoxon signed rank test, $n = 8$, $z = -2.524$, $P = 0.012$). Interestingly, the difference in absolute mass was related to time in a significant way (Spearman rank-order correlation, $r = 0.733$, $P = 0.014$) as was the percentage change in mass (mass difference between captures / initial mass) ($r = 0.639$, $P = 0.008$) (see Section 1.5 for life history observations).

Chorus patterning

The three-dimensional plot (Fig. 4.1a) and quadratic smoothing (Fig. 4.1b) of residency rankings on burrow localities revealed a systematic gradient, with a trend for transitory and enduring males to be found on opposite ends of the study site. A matching plot and smoothing approach to the distribution of body mass over burrow position on the study site presented a more complicated relationship (Fig 4.2a,b). Here, opposite ends of the study site were characterised by either light or heavy resident males, with individuals of average mass being found in the core area. Lastly, the plot and quadratic smoothed figures (Fig. 4.3a,b) of SPLs on burrow localities showed a regular hyperbolic trend across the study site, with louder males being found mostly on the study site boundaries. There was no tendency for mated males to be closer to the centre of the chorus aggregation (Mann-whitney U test : $U = 23$, $n_1=3$, $n_2=12$, $P = 0.631$) (Fig 4.4). Systematic patterns of residency, body mass and the sound pressure of males were thus recognized.

4.3 Discussion

The results from this study showed that there was non-random mating in *P. kochi*, with mated males being individuals with the higher calling rates and the most dynamic burrow activity. More frequent calling males are also, counter-intuitively, the most persistent chorusing participants on the study site. The interaction between call rate and residency appeared to affect mating success.

Although assessing the significance of quadratic spatial landscapes and three-dimensional plots are difficult, the systematic patterning witnessed in these plots are suggestive of biologically interesting relationships. First, a residency gradient appeared to run across the study site, with enduring males found at one end of the study site and transitory males found at the other end. Interestingly, mated males are anomalous in being the more permanent residents in the area characterised by brief chorus tenures of other males. This may imply space pre-emption by more permanent territorial males. Second, the mass patterning of males over the study site revealed that average massed individuals were found in the core chorus area, with opposite ends of the study site being characterised by either heavy or light males. Lastly, patterning of male SPL showed a regular hyperbolic trend across the study site, with softer males being found located in the core chorus area, and louder males being found on the periphery. It is interesting to note that the core area is the most densely populated on the study site, and that the males found in this area are characterised by both average mass and lower than average SPLs.

The demonstration of nonrandom patterns of mating cannot be considered sufficient proof for the presence of mate choice because assortative mating may arise for other reasons (Arak 1983, Halliday 1983, Parker 1983, Maynard Smith 1987). Correlational studies of mate choice are plagued by the possibility that females are choosing the territory of a male rather than any specific male characteristic, and that selection of a male is determined by male-male interaction and not by female choice per se (Gibson *et al.* 1991, Wiley 1991). However, there seemed to be no obvious territorial features or placement on

the chorus that distinguished mated from non-mated males, besides the number of burrow entrances utilised by any one male. Also, the proximity to the chorus centre had no effect on mating success (i.e. no evidence for 'hotspots' *sensu* Bradbury *et al.* 1986).

Although several significant correlates of mating success were identified in *P. kochi*, it would be incorrect to conclude that any one of these were critical mating cues. All potential cues were not measured, and other unmeasured correlates of burrow locality and quality, phenotypic characteristics or vocalisation features could be the object of female choice. What is clear from these results, however, is that some aspect of chorus activity, or something that is strongly correlated with it, was important to females.

This study suggested that male mating success is associated with high nightly display rate, prolonged chorus site tenure, and elevated levels of burrow activity. The implication that mate choice may be based on display performance raises several interesting issues. If females choose between males on the basis of display rate and chorus attendance, then what prevents all males from performing at successful levels? The obvious question to ask is : what is setting the limits to male behaviour? Correlational evidence suggests strongly that energetic factors play an important role. Chorusing *P. kochi* individuals lose weight during the breeding season, the extent of which is dependent on the length of chorus site tenure. Decrease in body mass suggests that the expenditure of energy by male barking geckos is greater than their energy uptake during breeding activity. This trend is common among prolonged breeding anurans (Wells 1978, Morton 1981, MacNally 1981, Given 1988). Significant differences in the mass and length measures and in foraging strategies between vocal and non-vocal adult *P. kochi* males were also found. Regular chorus activity must entail high energetic expenditure.

Burrow activity, call rate and chorus tenure all reflect the amount of energy an individual is able to devote to mating activity and may thereby indicate the health of that individual (*sensu* Hamilton & Zuk 1982), or they could be advertising the quality of the male in general (Zahavi 1977, Andersson 1982). Reaching the age of sexual maturity might in itself be understood as a condition-dependent trait that may contribute to the honesty of the signal. More applicable to this study though is the idea that changes in body mass will reflect physical

condition and the ability to tolerate weight loss occurring during the prolonged mating season (Ruby 1984). Variation in male *P. kochi* advertisement behaviour might be due to inherent viability differences of males in the population.

The hypothesis that variation in calling output may be understood by the differential abilities of males to support this behaviour was tested by Sullivan (1982). Sullivan showed that while male toads (*Bufo woodhousei*) varied significantly in their call repetition rates, the rank order of the male's call rates was consistent between chorus nights. Furthermore, females preferred males with higher repetition rates. It was suggested that if females chose males that were better able to physiologically tolerate the stresses associated with calling behaviour (those with 'good genes'), and if the variation in physiological fitness has a heritable basis, then female choice for faster calling males would evolve through the advantage derived to their offspring from having superior fitness. Investigations revealed that there was no relationship between call rate and maximum aerobic capacity, during forced activity, of males with known call rates (Sullivan & Walsberg 1985). However, maximum aerobic scope might not be the most appropriate measure of viability fitness.

In many studies, reproductive activity or success is positively correlated with age (Manning 1985, Grahn & Von Schantz 1994). Life history theory suggests that regardless of the level of reproductive effort, if young males have low mating success then selection should favour males that initially keep their reproductive effort low by either reducing reproductive activity, or by delaying the onset of reproduction (Williams 1966, Pianka & Parker 1975, Lessells 1991). Also, if vocalising is energetically costly then it is expected that smaller males should invest more time in growth rather than reproduction. Studies in mammals, fish and anurans that have managed to quantify the reproductive activity of young males, have all demonstrated negative relationships between the level of reproductive activity, and growth, survival or time spent foraging (Clutton-Brock *et al.* 1982, Warner 1984, Given 1988). The observation of a phenotypic 'threshold' in body mass that needs to be crossed before *P. kochi* males begin chorusing is in accordance with such theory.

The most interesting result of this study was the presence of a significant positive relationship between call rate and residency. This relationship is unexpected because it is

energetically more costly to display constantly. This positive relationship may be due to both traits being condition-dependent. The observation that mass loss is proportional to time spent chorusing, and differs significantly between callers and non-callers supports the claim that the relationship between call rate and residency is due to variation in male condition. It is important to realise, however, that the knowledge of secondary sexual traits being conditional means only that males in good condition are capable of attracting females. These characters are honest signals in the sense that low quality males cannot cheat and signal high quality (Zahavi 1975). Before 'good genes' selection can unequivocally be invoked, however, it must be shown that females mating with males bearing such viability traits confer a viability advantage to their offspring (Møller 1994).

The finding that male mating success is closely linked to individual differences in chorus behaviour and activity, and display effort, and less to morphological or territorial placement characteristics suggests that an intersexual component does exist in the gecko system. Females mating with more persistent males seem to be more likely to mate with males in better condition. The observation that vocal display in *P. kochi* appears to be condition-dependent is consistent with the evolution of handicap signals. In terms of its present evolutionary function then, these results suggest that female choice for good genes, and as yet unidentified direct benefits, may be responsible for costly male behaviour.

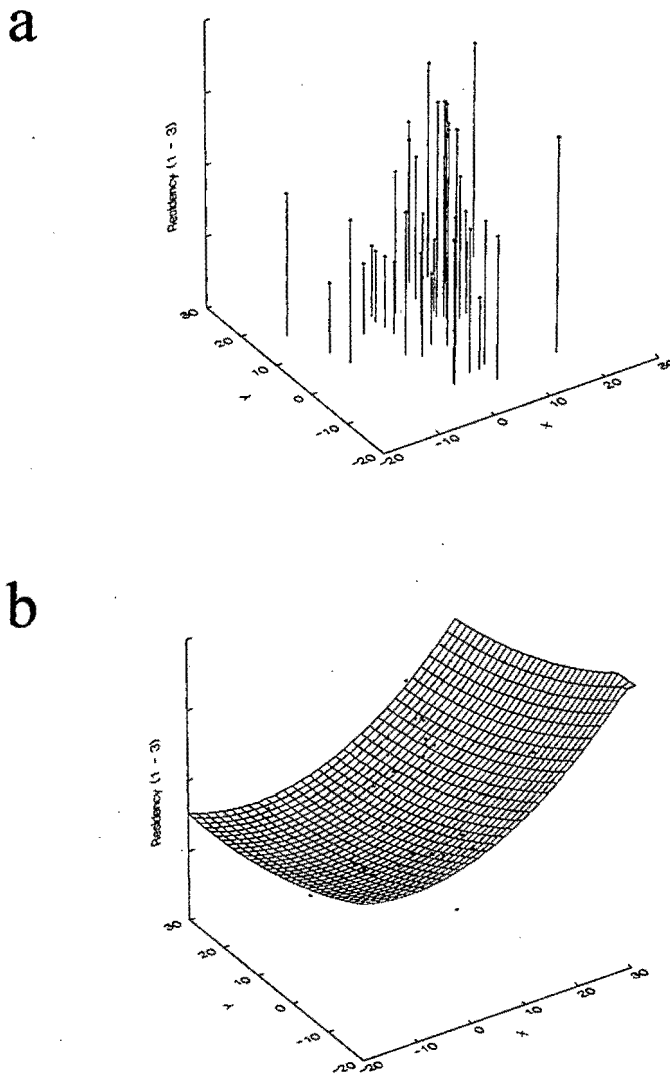
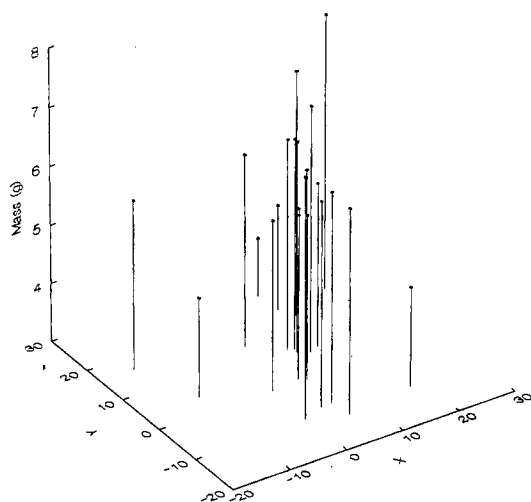


Fig. 4.1 Three-dimensional plots of residency rankings over the spatial distribution of burrows on the study site : (a) spike-plot and (b) quadratic surface smoothing. X and Y dimensions represent 2-dimensional Euclidian space. Units for these dimensions are in metres.

a



b

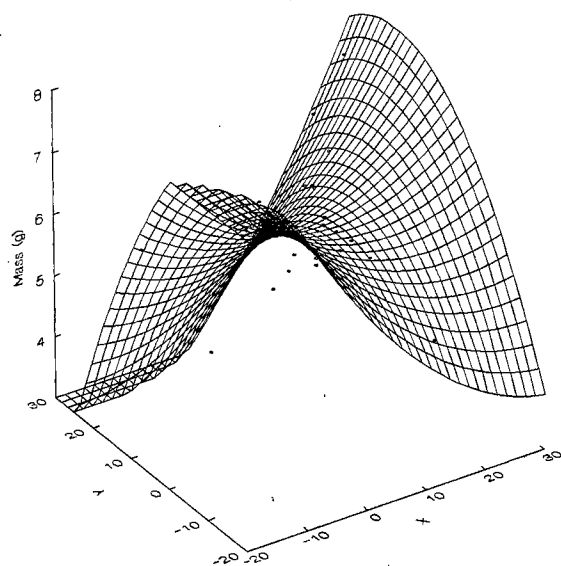


Fig. 4.2 Three-dimensional plots of mass over the spatial distribution of burrows on the study site : (a) spike-plot and (b) quadratic surface smoothing. X and Y dimensions represent 2-dimensional Euclidian space. Units for these dimensions are in metres.

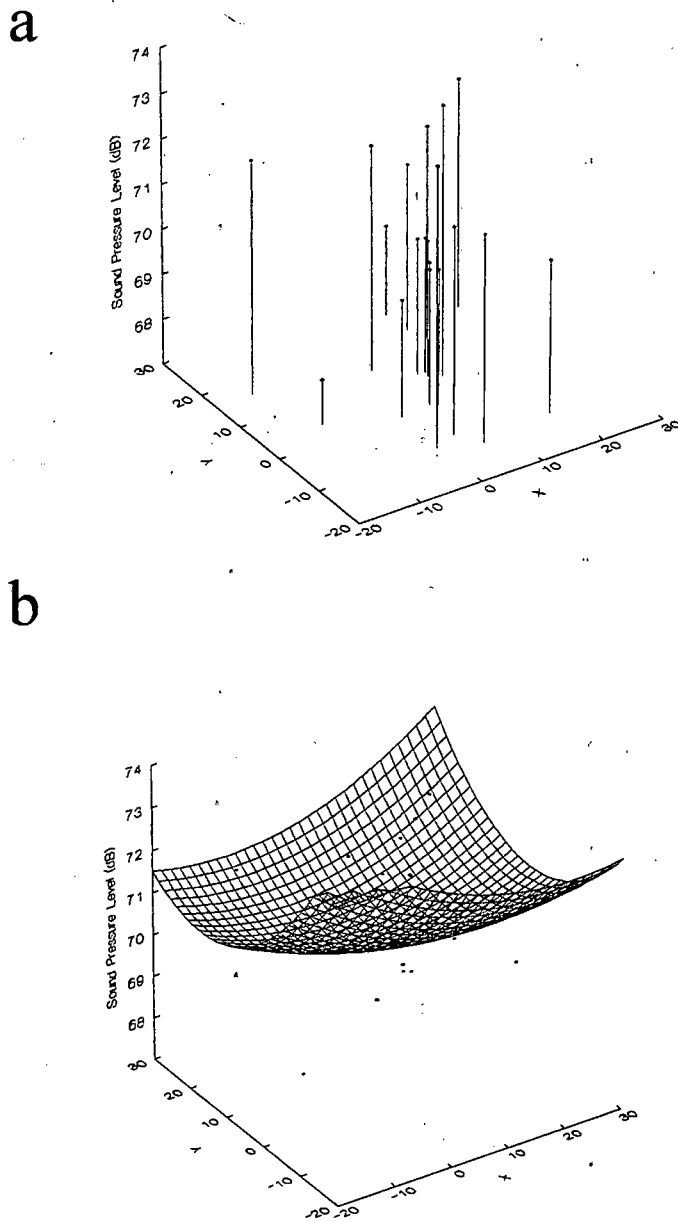


Fig. 4.3 Three-dimensional plots of SPL over the spatial distribution of burrows on the study site : (a) spike-plot and (b) quadratic surface smoothing. X and Y dimensions represent 2-dimensional Euclidian space. Units for these dimensions are in metres.

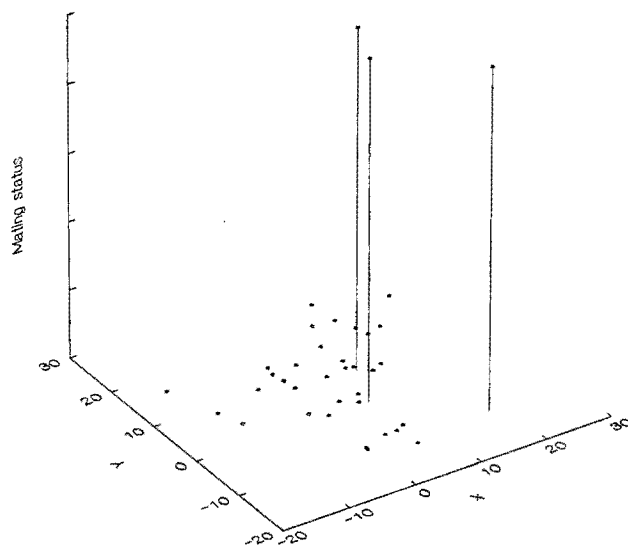


Fig. 4.4 A three-dimensional spike-plot of mated male's localities within the study site area. X and Y dimensions represent 2-dimensional Euclidian space. Units for these dimensions are in metres.

SECTION 5

Synthesis

5.1 The species of *Ptenopus*?

Barking geckos are presently thought to be represented by three species in southern Africa (Branch 1988). However, upon closer inspection of the literature, several subtle but important discrepancies in the logic by which taxonomic status has been accorded to species in the *Ptenopus* genus are apparent. These are highlighted further by the findings of this present research, and are discussed here in some detail.

Past research suggested a wide range of key features that have been used to distinguish between the three species of *Ptenopus*. These features are summarised in Table 5.1. Brain (1962) distinguished between *P. garrulus* and *P. carpi* primarily on the extent of toe fringing, habitat type, number of labial scales, nostril openness and the presence or absence of a pigmented peritoneal lining. Several other differences were noted, and these included the number of clicks present in each species' call. Similar characters were used to discern between the same two species when Haacke (1964) described the presence of a third species, *P. kochi*. *Ptenopus kochi* was identified by the presence of elongated pointed finger scales and small body scales.

There were several notable differences used in the revisions made to the features considered most useful in separating *P. carpi* from *P. garrulus* (Haacke 1964). First, the number of labial scales was dropped as a character and instead the number of scales around mid-body was adopted as a more informative feature. Second, the habitat preference of *P. garrulus* was expanded to include a range of mixed sand and gravel substrates. Lastly, vocalisation features of *P. carpi* were modified to included a far greater range of clicks in any one call. A similar revision extending the range of click number of both *P. carpi* and *P. kochi* was again made in 1969 (Haacke 1969). The importance of toe fringing, pigmentation of the peritoneal lining, and habitat type for these two species were still retained as useful species descriptors. Later work again separated two subspecies of *P. garrulus* (*P. g. garrulus* and *P. g. maculatus*) based on colouration differences, and differences in the number of scales around mid-body (see Table 5.1) (Haacke 1975).

Besides obvious differences in toe scaling, body scale size and in mean click number, sonographic investigations conducted in this present research revealed several spectral features of the calls of *P. garrulus* and *P. kochi* that reliably tell them apart. These features have not been explicitly reported in previous studies. The call of *P. kochi* is made up of a stereotyped series of clicks, with several unmodulated harmonics distributed between a lower and an upper frequency range (see Section 3.1). Conversely, the vocalisation of *P. garrulus* is made up of a clearly frequency-modulated series of harmonics, and only the clicks after the second are stereotyped (Fig 5.2). The first click differs from the rest in being considerably more modulated, louder and longer. In this study, calls of both types were recorded, and toe-clippings from the actual males used in recordings obtained. Such a coupled investigation of sonographic analysis with toe examination is surprisingly novel in the history of study on this genus. The shape of the scaling proved to be a reliable indicator of the species status of these individuals (Plate 5.1).

The reality of the differences between *P. kochi* and *P. garrulus* are thus clear. However, the evidence for the distinctiveness of *P. carpi* as a separate species is unfortunately not as clear. In a plenary paper, Brain revised the status of *P. garrulus* and identified a new species - *P. carpi* (Brain 1962). When Haacke (1964) introduced *P. kochi*, he suggested that Brain's previously recognised *P. garrulus* consisted of both *P. kochi* and

P. garrulus. *Ptenopus carpi* was set apart by differences in toe fringing, call click number and the absence of pigmented peritoneal lining.

Haacke's later work on *Ptenopus* shed doubt as to the importance of an unpigmented peritoneum being unique to *P. carpi* when it was noted that the peritoneum was not always pigmented in *P. garrulus* (Haacke 1975). This finding should have suggested that the morphological features in *P. garrulus* were not as invariant as previously assumed, and that variation in the characteristics used for classification of the *Ptenopus* genus should have been investigated further. However, this finding was ignored.

Besides the structure of toe fringing and call click number, *P. carpi* and *P. g. garrulus* (noted as being sympatric in the Gobabeb area) are, in fact, indistinguishable. Both species share similar habitats (gravelly substrate preferences) and overlap considerably in the number of mid-body scales (see Table 5.1). Researchers have argued that each of the three species has a distinctive call, with click number and pulse repetition rate (duration) being the key distinguishing features (Haacke 1964, 1969, Branch 1988). However, in the light of the argument presented above and the findings of Section 3, it is interesting to re-examine these claims. First, it is informative to realise that most work describing the number of clicks in any species' call and call duration have been anecdotal, relying on written records of click number from different localities (c.f. Haacke 1969). The click number of *P. kochi* is high and its call rate fast, and it is exceptionally difficult, if not impossible, to accurately establish the exact number of clicks in any one call without spectrographic analysis. The belief that *P. carpi* possesses a similar call to *P. kochi* must confirm that spectrographic analysis is also essential for accurate data relating to the call features of *P. carpi*. While written records of frequency data on the click number present in *P. garrulus* are more than likely to be reliable, similar documentation for *P. kochi* and any other species with a similar call must be viewed with extreme caution. Surprisingly, no recordings have ever been made of the call of *P. carpi*. The vocalisation characteristics of *P. carpi* from various localities in Namibia is based solely on verbal reports (Brain 1962).

Second, the sonographic analyses of Section 3 reveals that the distribution of click number of the call of *P. kochi* is normally distributed (Kolmogorov-Smirnov goodness-of-fit

test; $D_n = 0.038$, $n = 300$, $P = 0.336$). Click number ranges from 6 - 18 clicks, has a mean of 12 clicks and a standard deviation of 1.554 clicks. The range of click number documented here clearly overlaps with that noted for *P. carpi* (see Table 5.1). By constructing confidence intervals of *P. kochi* click number, it can be seen that click number is rarely expected to deviate substantially from this value of 12 clicks ($SE = 0.0897$, d.f. = 299, 95 % confidence intervals = 12 ± 0.177 clicks). Click number was also seen to be independent of temperature (Section 3.2.4) whereas call duration was not (Section 3.2.3). The temperature at which this sample was taken ranged from 15.4 °C to 28.7 °C. The independence of click number on temperature cannot be extrapolated beyond these values.

Lastly, it is also important to note that while onomatopoeic reproductions (see Table 5.1) might help relay the general impression of a call (e.g. Haacke 1969), they cannot serve as a reliable basis for species identification, and they do not supply any information relating to call features (i.e. duration). The call of both *P. kochi* and *P. carpi* are described as a monotonous series of clicks ("gack..gack..gack"), those of *P. carpi* being slower than *P. kochi* (Haacke 1969). However, on a cool evening, the call of *P. kochi* is expected to be of slow duration (see above). On these three grounds, it appears unrealistic to consider the call of *P. carpi* distinctive. In fact, estimates of the call features of *P. carpi* must be viewed essentially as guesswork until actual recordings are obtained.

At present, the only character remaining a potentially reliable predictor of *P. carpi* seems to be its weakly fringed toes. It is important to ask whether the extent of toe fringing is a strong enough character to afford *P. carpi* its distinctive species status. There is an obvious correlation between the degree of softness of the substratum and the increased surface area of species' digits. *Ptenopus kochi* has the largest digit surface area available and burrows in the soft sand of the inter-dune spaces, and in the silt of the actual river bed. The lateral fringes of elongate scales on *P. kochi*'s digits probably assist the gecko when walking over unstable surfaces of loose sand by reducing sinking, and by facilitating digging. *Ptenopus garrulus*, with a smaller digit surface area, appears relatively indifferent to the substrate hardness, but seems to avoid softer sand and hard ground. *Ptenopus g. maculatus* inhabits those parts of Namibia and the Northern Cape which are below the 500 mm rainfall zone (Haacke 1975). In this area, the substratum varies considerably, from

compact and hard through limy soil to gritty sand and fine gravel. *Ptenopus carpi* is known only from north of the Kuiseb river, in areas where the annual average rainfall falls below 125 mm and where the soil is hard. Its preferred habitat appears to be gently undulating gravel plains.

There is the possibility that toe fringing is phenotypically plastic, where a single species genotype produces a range of toe phenotypes depending on substrate conditions. There is a large body of evidence to suggest that such plasticity exists in many life history traits (reviewed in Lessells 1991). The patterns of variation of toe scaling of *P. garrulus* remain to be investigated. Observations from *P. kochi* suggest that there is a notable amount of variation in the degree of lateral fringing of toes and fingers, with some individual's digits being more extensively fringed than others, although the presence of elongated scales was invariant in the sampled population of *P. kochi*.

While it was impractical to have pursued the taxonomy of this genus further in this research project, it would be prudent to examine aspects of vocalisations of *P. carpi* more thoroughly with the aim of ultimately investigating the degree of reproductive discontinuity and genetic divergence between *P. carpi* and the other two species. Given the inadequacy of knowledge concerning vocalisation features of *P. carpi*, the questionable use of most of the key historical features used to discern *P. carpi* from other species in the genus, and a dearth of knowledge concerning the developmental basis of toe fringing in these animals, the presence of *P. carpi* must remain an open-ended question for the moment. Indeed, the three species of *Ptenopus* may ultimately require revision.

5.2 Synthesis

This study has been an attempt to develop and expand our knowledge concerning the functional significance of the little understood communication system of Koch's barking gecko, *P. kochi*. In this study, I have approached all questions regarding the adaptive value of individual behaviour through an appeal to the epistemological necessity of the

adaptationist approach (*sensu* Williams 1966, Brown 1982). Here, the assumption of evolutionary adaptation manifest in the behavioural patterns of *P. kochi* was used as a means to develop falsifiable working hypotheses, and not, as the common critique argues, as a tenet of faith (Gould & Lewontin 1981). Furthermore, a non-historical definition of adaptation (*sensu* Reeve & Sherman 1993) was adopted for questions in this research in order to decouple the study of adaptation from the study of the evolutionary mechanisms that generated them.

Several fundamental questions regarding the adaptive value of *P. kochi* behaviours were posited subsequent to an initial exploratory observational period. A diagrammatic flow chart summarising several of the more significant observed life-history stages of *P. kochi* is provided in Fig 5.1. Preliminary observations revealed that chorusing males did not actively forage, and were spatially distinct from foraging females and foraging non-calling males. Furthermore, vocalising males behaved in ways that suggested territorial competition between them, and females wandering into the chorus area from time to time displayed active mate-sampling behaviour which was implicative of mate-choice. The original objective of this research was to generate and to test multiple-working hypotheses relating to the vocalisation and mate-selection patterns evidenced in the *P. kochi* system. Since this is the first investigative study of its kind on *P. kochi*, this research plainly generated more questions than it did answers, although in several important respects, I believe that the initial objective has been satisfied.

First, this present research program substantiated the assumption that *P. kochi* males were territorial. Observations suggested that the number of calling territories were limited over the study site as there was a virtual constancy in the number of active callers in this area, despite considerable turnover in the identity of these individuals. An analysis of nearest-neighbour spacing in male aggregations showed clearly how this patterning reflected the occurrence of regularity. Such spacing was attributed to inter-male interaction and territoriality. The nature of acoustic interactions between neighbouring males was first analytically explored, and the intensity mechanism for inter-male spacing was finally verified through the use of playback experiments. Results from investigations into competition in *P. kochi* highlighted the importance of residency effects influencing both the size of shared

acoustic space (more permanent individuals had average-sized spaces) and the likelihood of a male displaying offensive behaviour in the face of territorial intrusion. Despite suggestions to the contrary (Ruby 1984, Tokarz 1985), there was no tendency for heavier or lengthier males to have larger (acoustic) territory sizes or to be the most aggressive. However, heavier males did have louder calls, although this did not translate into significantly larger shared acoustic space.

Second, the variation manifest in the vocalisation of *P. kochi* was studied in an attempt to understand how temporal and spectral features predictably covaried with both intrinsic and extrinsic sources of variability. Call descriptor measures were seen to covary significantly with both meteorological variables and with individual morphology. The bases of inter-call differences were explored in an analytical investigation where the confounding influences of call descriptor covariation with intrinsic and extrinsic sources of variability were statistically removed. This analysis revealed that while the non-covariate-adjusted procedure might suggest individuality of signal structure in the gecko call, once covariance was removed, the calls were rendered statistically indistinguishable from one another. Nightly chorus duration was also seen to be predictable based on daily meteorological determinants.

Lastly, the possibility of mate choice acting in the mating system of *P. kochi* was studied in a correlational investigation. Heavier and lengthier males were not the target of female choice. Interestingly, males of average-length and body mass were the most permanent members on the chorus site. These males were well characterised by having average-sized acoustic spaces, and significantly higher call rates. They also differed significantly in their pronounced level of burrow entrance activity. They were also the ones most likely to mate on the chorus site. The manifestation of vocal activity in *P. kochi* was seen to display features characterised by classical condition-dependence (Zahavi 1977, Grafen 1990). Here, call rate was positively related to the permanence of chorus site tenure in a system where energetic limitations appear to constrain the expression of vocalising.

The *P. kochi* mating system is resource based, with mated females residing in male's burrows, and juvenile offspring remaining in their natal father's burrow system for several

weeks following hatching. Studying correlates of mate choice is inherently difficult since the phenotypic characteristics of males are expected to vary in the same direction as call rate and chorus site tenure, and these characteristics are also likely to be confounded with aspects of territory quality (many of which remain unmeasured). Any benefits to females of mate choice based on the phenotypic expression of males might be surpassed by direct benefits for male resources. However, the likelihood of costly male vocal behaviour functioning presently in the maintenance of 'good-genes' in the population must be considered a potential prospect. Better quality males might benefit by translating rarely acquired food resources into vocal display in increments which are disproportional to that occurring in other males. Females mating with physiologically more capable males would benefit indirectly if this capacity to support the stresses of vocal activity was heritable, since male progeny created through such matings would bear the physiological competence of their father. All that is required for this evolutionary process to occur is for there to be conformity between heritable genetic variation of males and patterns of variation of female choice (Møller 1994).

Although the mating system of *P. kochi* is resource-based, the actual basis for this resource is not well understood. Certain male burrows might be better places for females to leave their eggs in, and some feature of egg viability might correlate with territorial placement or territory size. Burrow structure or positioning might be related in some way to the probability of hatching. The importance of a nest environment that dampens temperature fluctuations is clear in a range of lizard species (Overall 1994). Burrow depth is known to be associated with a decreasing range in the thermal profile, and with a lower probability of egg desiccation. Female *P. kochi* might prefer laying eggs in deeper burrow systems for this buffer effect. Unfortunately, the structure of male burrows were not investigated, owing both to the non-destructive investigative constraints imposed by the research Ministry in Namibia, and by simple ethical considerations. The Kuiseb river is also subject to episodic flooding, although this is infrequent (once every four or five years). Some burrow systems might be better positioned to avoid structural decimation when flooding occurs. One would expect that burrow systems least likely to be influenced by flooding to be situated away from the river bed towards the dunes. However, males

residing in the area close to the dunes are likely to suffer structural difficulties in constructing burrows in the loose sand.

Certain areas on the chorus site might also be safer places from which females could leave to go and forage, or offer closer proximity to more profitable foraging areas. *Ptenopus kochi* is likely to be preyed upon by a variety of predators, including *Bitis caudalis* (horned adder), and two species of *Psammophis* (sand and whip snakes), all diurnal species in the Gobabeb area. Remains of barking geckos are also known from owl pellets (Nel & Nolte 1965). Predation may account for the high turnover and disappearance of individuals within and between field seasons on the study site. The incidence of observed predation during the 1995 field season was negligible, although it is expected that even if a high level of predation is occurring, most of it is likely to remain unobserved. The extent and complexity of a territorial site is likely to correlate with its ability to act as a better predator refuge (Stamps 1983b). It is possible that since females were observed choosing males having both a larger number of open burrow entrances and a greater number of burrow entrances than other males, these choices might relate to the predation avoidance properties of the male burrows.

It can be speculated that since most foraging occurred under an *Acacia* tree situated in the middle of the study site, this area was a profitable foraging ground. If female choice is based on the convenience of proximity to a suitable foraging site, then it would be expected that most matings should occur in close proximity to this area. Furthermore, the extent of male aggregation was highest in this area, suggesting that there was some reason why males were most competitive here. However, observed matings did not display any significant tendency of being associated with distance from the chorus centre. Before proximity to the foraging centre can be ruled out as a prospective causal explanation for patterns of mate-selection, it is necessary for further research to concentrate on obtaining more data on female mate site selection.

It might appear obvious that males having longer chorus site residencies are, by a simple function of probability, more likely to be the ones that females encountered when they wandered into the chorus area and therefore the ones that females mate with. This might

have been the case if the available chorus sites over the study area had not been continually saturated with calling males. Females entering the chorus area were always presented with a range of potential calling mates, and females did sample several males before picking and settling with one.

Another possibility is that females are selecting mates based on the fact that males which are more permanent may be more likely to afford both themselves and their offspring some form of direct safety benefits - either through mate or egg guarding. While RHP of males did not seem to be related to any morphological measures, more permanent males were clearly the more aggressive males. The prior resident effect (Maynard Smith & Parker 1976) is a well documented phenomena (Riechert 1979, Davies 1978, Haley 1994, Leuck 1995), although interpretations as to why a prior owner of a resource is more likely to behave aggressively in a contest vary widely. The intriguing observation that more permanent males were the ones more likely to display aggression during playback experiments suggests either that such males might be better potential defenders of burrow resources (including females and eggs), or conversely, be defending important burrow resources (e.g. eggs from previous females). Although only one of the three males displaying aggression had mated prior to playback experiments (and none of the five males failing to display aggression had mated), there is the possibility that these males were guarding eggs from past matings. In this situation, the payoff asymmetry between males defending eggs would likely exceed that of intruder individuals, giving rise to an understandable propensity for aggression in defenders. Aspects of RHP and payoff asymmetries between males and correlates of burrow resources warrants further attention. It would also be interesting to know whether competing males pose a predation threat to the eggs in other male's burrows.

On the opposite extreme of any resource-based arguments for the evolution of the *P. kochi* mating system, is the possibility that the size of a burrow system is an ornament in itself. Sexual selection could then favour the evolution of males making bigger burrows. Unless there is some clear identifiable resource that burrows provide, it cannot be stated

definitively that burrows provide direct benefits to females. It is conceivable that all the attributes of mated males that have been outlined are simply multiple correlates of quality.

Further prospects for research on *P. kochi* ?

Firstly, and as obviously implied by the discussion above, further research needs to be directed at aspects of mating success in *P. kochi*. While the low frequency of mating in the population is sufficient for statistical inferences, the correlational evidence recorded is not sufficient to infer causality of any of the hypothesised mechanisms of mate-choice. Burrow excavation and measurements are likely to yield a set of as yet unconsidered hypotheses for both aspects of mate choice and male competition. More data need to be collected on female mate site selection in order to understand the influences of proximity to the chorus site (foraging) centre and correlates of male burrows features. The bases of female acoustic preference also require further investigation. Ideally, controlled female phonotaxis experiments need to be set up to obtain a more convincing answer to the question of female preference in the *P. kochi* system. However, despite the low rate at which females entered the chorus to mate, it is almost impossible to know when such an event is likely to occur. This makes studying the acoustic bases of female choice logistically troublesome under natural conditions. It may be possible to isolate and feed a sufficiently large number of females in either natural enclosures or in the laboratory at the early onset of the breeding season. Changes in body mass, hormone or behavioural profiles might be useful indexes with which to gauge the extent of female receptivity. Once females are ready to mate, their responses in a phonotaxis arena to trials presenting different auditory cues could then be tested.

As well as studying the bases of female mate choice, it would be useful to learn more about facets of male territoriality and competition. Carefully designed removal experiments of actively vocalising males on the chorus site are likely to provide a better understanding of the level of territorial saturation, as well as differences between established callers and unsuccessful non-caller individuals. Hormones can also be used to manipulate the behavioural phenotypes of free-living geckos. Levels of aggression and display behaviours have successfully been manipulated in a number of lizard species by manipulating testosterone levels (reviewed in Marler *et al.* 1995). In this way, the costs and benefits of

aggression and defence of burrows can be investigated. The energetics of calling also needs to be investigated further in order to better understand the possible basis for differential male chorus performance. It would be interesting to know whether the amount of available energy or the ability to utilise energy to support calling behaviour constrains a male's ability to partake in calling. It is necessary to understand whether physiological differences among males is responsible for the observed differences in calling behaviour, or whether calling performance is correlated with the general physiological condition of males. General physiological condition can be evaluated by measures of whole-animal performance (e.g. VO_2 , haematocrit) (Bennett 1986), while the relationship between the physiology of males and their ability to sustain calling activity needs to be addressed with slightly different measures (e.g. muscle mass, glycogen stores) (Ryan 1988).

Several months of exploration has unveiled many interesting facets to the study of chorus organisation and mating preference in *P. kochi*, and has at the same time, opened up a range of new and pertinent questions necessary for a more complete understanding of the mating system of *P. kochi*. The possibility now exists to explore some of these questions in an experimental fashion. Further studies on this enigmatic animal may yield some fascinating answers.

Table 5.1 Historical taxonomic features used to distinguish between the three envisaged species of *Ptenopus*.

Features	<i>P. garrulus</i>	<i>P. koehi</i>	<i>P. carpi</i>	Reference
Morphology	- Toes and fingers strongly fringed with spinose scales, those on toes being long and comb like.		- Digits weakly fringed but strongly clawed and fringed laterally with spinose scales. Toes larger than fingers.	Brain 1962
Habitat	- Sandy habitats of soft river deposits		- Gravel plains	
Vocality	- Click range 4-5		- Up to 8 clicks?	
Other	- Peritoneal lining pigmented, few labial scales : upper 6-9 lower 6-10		- Peritoneum unpigmented, labials more numerous : upper - 10 lower - 13	
Morphology	- Toes strongly fringed laterally, fingers fringed with pointed triangular scales.	- Toes strongly fringed laterally, fingers fringed with elongated pointed scales.	- Toes weakly fringed laterally	Haacke 1964
Habitat	- Mixed habitat, but avoiding river bed sand	- Sandy river bed	- Gravel plains	
Vocality	- 4 - 6 clicks, first click is pronounced	- 9 - 11 clicks, monotonous	- Up to 16 clicks ? monotonous ?	
Other	- Pigmented peritoneum, 120 - 146 scales around mid-body	- Pigmented peritoneum, 187-222 scales around mid-body	- Unpigmented peritoneum, 105 - 131 scales around mid-body	
Vocality	- 3 - 6 clicks, average = 5 or 6 sample = 9 calls, "Squee-chi-chi" or "Gack..gack.gack"	- 9 - 16 clicks, average = 11 or 12 sample = 8 calls, rapid and monotonous	- monotonous series of up to 16 clicks ?	Haacke 1969

Morphology	- Fingers have serrated edges, toes are edged with well developed comblike fringes.	- Depressed toes and fingers fringed by combs of elongated pointed scales.	- Compressed fingers without a fringe of elongated scales. Fringe along edge of toes is poorly developed.	Haacke 1975
Habitat	- Sand (<i>garrulus</i>) or gravel (<i>maculatus</i>)	- Sand	- Gravel plains	
Vocality	- NO DATA	- NO DATA	- Up to 20 clicks, slowly repeated ?	
Other	- Peritoneal lining usually pigmented, <i>garrulus</i> has 146-194 scales around mid-body, <i>maculatus</i> 116-168	- Pigmented peritoneal lining, 187 - 226 scales around mid-body	- Unpigmented peritoneal lining, 105 - 131 scales around mid-body	
Morphology	- Strongly fringed toes	- Fringed toes with elongate scales	- Weakly fringed toes	Branch 1988
Habitat	- various soil substrates	- Sand	- Gravel plains	
Vocality	- 1 - 13 clicks, average = 5	- NO DATA	- 3 - 20 clicks, usually 12 ?	
Other	- 110 - 190 scales around mid-body	- 187 - 222 scales around mid-body	- 105 - 140 scales around mid-body	
Morphology	- Fringed toes with triangular scales	- Fringed toes with elongated pointed scales	- NO DATA	Present study
Habitat	- Gravel plains	- Sand	- NO DATA	
Vocality	- 3 - 6 clicks, average = 4 or 5, sample = 30 calls	- 6 - 18 clicks, average = 12, sample = 300 calls	- NO DATA	

a



b



Plate 5.1 Photographs of toe-clippings of (a) *P. kochi* and (b) *P. garrulus*. The toe of *P. kochi* is fringed with elongate pointed scales, whereas the toe of *P. garrulus* is fringed, but with triangular scales.

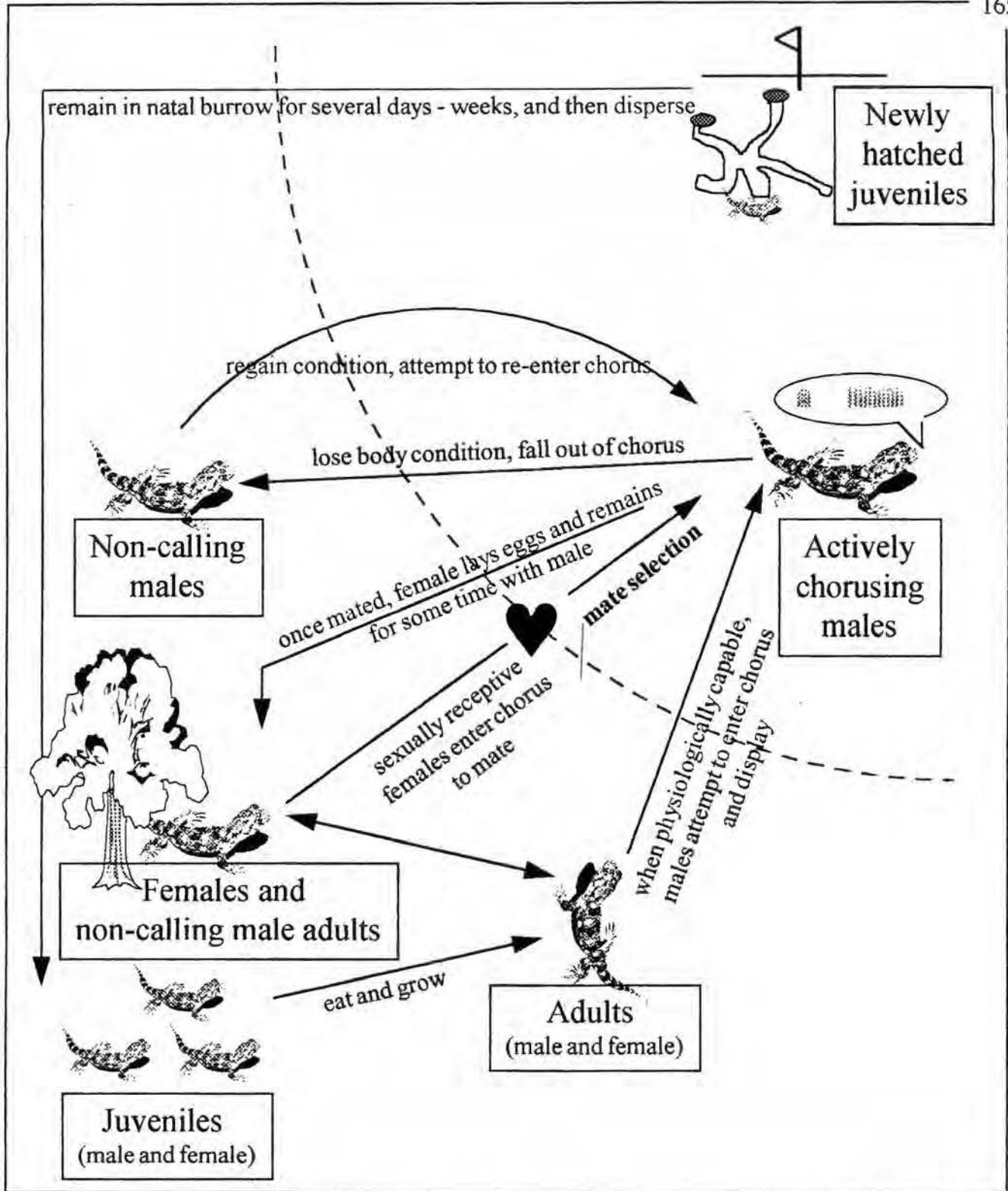


Fig. 5.1 A diagrammatical flow chart of the observed life-history of *P. kochi* individuals at several significant stages of their lives.

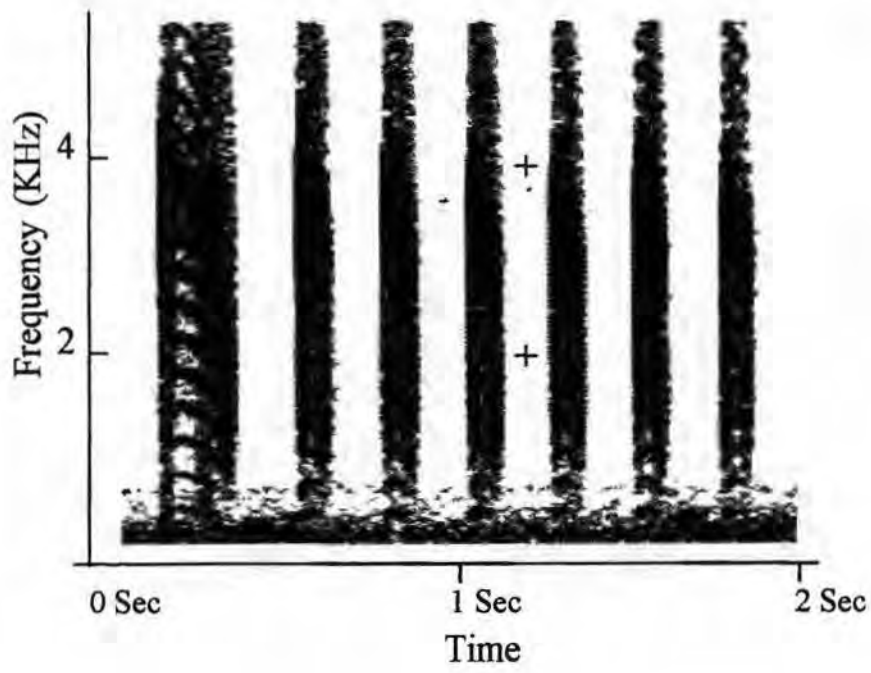


Fig. 5.2 A representative sonagram of the common barking gecko, *P. garrulus*.

References

- Alatalo, R. V., Lundberg, A. & Glynn, C. (1986). Female pied flycatchers choose territory quality and not male characteristics. - *Nature* 323, p. 152-153.
- Alatalo, R. V., Höglund, J. & Lundberg, A. (1991). Lekking in the black grouse - a test of male viability. - *Nature* 352, p. 155-156.
- Alexander, R.D. (1975). Natural selection and specialized chorusing behavior in acoustical insects. - In: *Insects, science and society* (D. Pimentel, ed). Academic Press, New York, p. 35-77.
- Anderson, R.A. & Vitt, L.J. (1990). Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. - *Oecologia* 84, p. 145-157.
- Andersson, M. (1982). Sexual selection, natural selection and quality advertisement. - *Biol. J. Linn. Soc.* 17, p. 375-393.
- Andersson, M. (1986). Evolution of condition-dependent sex ornaments and mating preferences : sexual selection based on viability differences. - *Evolution* 40, p. 804-816.
- Andersson, M. (1994). *Sexual selection*. - Princeton University Press, New Jersey.
- Andersson, S. (1989). Sexual selection and cues for female choice in leks in Jackson's widowbird

Euplectes jacksoni. - Behav. Ecol. Sociobiol. 25, p. 403-410.

Andrews, R.M. (1985). Mate choice by females of the lizard, *Anolis carolinensis*. - J. Herpetol. 19, p. 284-289.

Arak, A. (1983). Male-male competition and mate choice in anuran amphibians. - In: Mate Choice (P. Bateson, ed). Cambridge University Press, Cambridge, p. 67-101.

Arak, A. (1988). Female mate selection in the natterjack toad : active choice or passive attraction? - Behav. Ecol. Sociobiol. 23, p. 317-327.

Arnold, S.J. (1983). Sexual selection : the interface of theory and empiricism. - In: Mate choice (P. Bateson, ed). Cambridge University Press, Cambridge, p. 67-101.

Backwell, P.R.Y., Jennions, M.D., Christy, J.H. & Schober, U. (1995). Pillar building in the fiddler crab *Uca beebei* : evidence for a condition-dependent ornament. - Behav. Ecol. Sociobiol. 36, p. 185-192.

Baker, M.C., Thomson, D.B & Sherman, G.L. (1981). Neighbor/Stranger song discrimination in white-crowned sparrows. - Condor 83, p. 265-267.

Baker, R. (1978). The evolutionary ecology of animal migration. - Hodder & Stoughton, London.

Baker, R. (1983). Insect territoriality. - Ann. Rev. Entomol. 28, p. 65-89.

Balcombe, J.P. (1990). Vocal recognition of pups by mother Mexican free-tailed bats, *Tadarida brasiliensis mexicana*. - Anim. Behav. 39, p. 960-966.

Balmford, A. & Read, A.F. (1991). Testing alternative models of sexual selection through female choice. - Trends Ecol. Evol. 6, p. 274-276.

Barnard, C. J. & Burk, T. J. (1979). Dominance hierarchies and the evolution of 'individual

recognition'. - J. Theor. Biol. 81, p. 65-73.

Bateson, P (ed). (1983). Mate choice. - Cambridge University Press, Cambridge.

Bauer, A.M. (1990). Phylogeny and biogeography of the geckos of southern Africa and the islands of the western Indian ocean : a preliminary analysis. - In: Vertebrates in the tropics (G. Peters & R. Hutterer, eds). Museum Alexander Koenig, Bonn, p. 275-283.

Bauer, H. & Nagl. W. (1992). Individual distinctiveness and possible function of song parts of short-toed treecreepers (*Certhia brachydactyla*). Evidence from multivariate song analysis. - Ethology 91, p. 108-121.

Beacham, J.L. & Newman, J.A. (1987). Social experience and the formation of dominance relationships in the pumpkinseed sunfish (*Lepomis gibbosus*). - Anim. Behav. 35, p. 1560-1563.

Beaugrand, J.P., Payette, D. & Goulet, C. (1996). Conflict outcome in male green swordtail fish dyads (*Xiphophorus helleri*) : interaction of body size, prior dominance/subordination experience, and prior residency. - Behaviour 133, p. 303-319.

Beebe, W. (1944). Field notes on the lizards of the Kartabo, British Guiana, Caripito, Venezuela. Part 1 , Gekkonidae. - Zoological 29, p. 145-160.

Beecher, M.D. (1982). Signature systems and kin recognition. - Amer. Zool. 22, p. 477-490.

Beecher, M.D. (1989). Signalling systems for individual recognition: an information theory approach. - Anim. Behav. 38, p. 248-261.

Beecher, M.D., Stoddard, P.K. & Loesche, P. (1985). Recognition of parents' voices by young cliff swallows. - Auk 102, p. 600-605.

Beecher, M.D., Campbell, S.E. & Burt, J.M. (1994). Song perception in the song sparrow : birds

classify by song type but not by singer. - Anim. Behav. 47, p. 1343-1351.

Beer, C.G. (1969). Laughing gull chicks: recognition of their parents' voices. - Science 166, p. 1030-1032.

Beer, C.G. (1979). Vocal communication between laughing gull parents and chicks. - Behaviour 70, p. 1-2.

Belsley, D.A., Kuh, E. & Welsch, R.E. (1980). Regression diagnostics : identifying influential data and sources of collinearity. - John Wiley, New York.

Bennett, A.F. (1986). Measuring behavioural energetics. - In: Predator-prey relationships (M.E. Feder & G.V. Lauder, eds). University of Chicago Press, Chicago, p. 69-81.

Berry, J.F. & Shine, R. (1980). Sexual size dimorphism and sexual selection in turtles (Order Testudines). - Oecologia 44, p. 185-191.

Bishop, P.J., Jennions, M.D. & Passmore, N.I. (1995). Chorus size and call intensity : female choice in the painted reed frog, *Hyperolius marmoratus*. - Behaviour 132, p. 721-731.

Blakenhorn, H.J. (1972). Meteorological variables affecting onset and duration of calling in *Hyla arborea* L. and *Bufo calamita* Laur. - Oecologia 9, p. 223-234.

Borgia, G. (1979). Sexual selection and the evolution of mating systems. - In: Sexual selection and reproductive competition in insects (M.S. Blum & N.A. Blum, eds). Academic Press, New York. p. 19-80.

Bradbury, J.W. (1981). The evolution of leks. - In : Natural selection and social behavior (R.D. Alexander & D. Tinkle, eds). Carron Press, New York, p. 138-169.

Bradbury, J.W. & Gibson, R.M. (1983). Leks and mate choice. - In: Mate choice (P. Bateson, ed). Cambridge University press, Cambridge, p. 109-138.

- Bradbury, J.W., Vehrencamp, S.L. & Gibson, R.M. (1985). Leks and the unanimity of female choice. - In: *Evolution : essays in honour of John Maynard Smith* (M. Slatkin & P.J. Greenwood, eds). Cambridge University Press, Cambridge, p. 310-313.
- Bradbury, J., Gibson, R. & Tsai, I.M. (1986). Hotspots and dispersion of leks. - *Anim. Behav.* 34, p. 1694-1709.
- Bradbury, J.W. & Davies, N.B. (1987). Relative roles of intra- and intersexual selection. - In: *Sexual selection : testing the alternatives* (J.W. Bradbury & M.B. Andersson, eds). John Wiley, Chichester, p. 143-163.
- Brain, C.K. (1962). A review of the gecko genus *Ptenopus* with a description of a new species. - *Cimbebasia* 1, p. 1-18.
- Branch, B. (1988). Field guide to the snakes and other reptiles of Southern Africa. - Struik, Cape Town.
- Brenowitz, E.A. (1989). Neighbour call amplitude influences aggressive behavior and intermale spacing in choruses of the Pacific treefrog (*Hyla regilla*). - *Ethology* 83, p. 69-79.
- Brenowitz, E.A., Wilczynski, W. & Zakon, H. (1984). Acoustic communication in spring peepers : environmental and behavioural aspects. - *J. Comp. Physiol.* 155, p. 585-592.
- Bretagnolle, V. (1989). Calls of Wilson's storm petrel : functions, individual and sexual recognition, and geographic variation. - *Behaviour* 111, p. 98-112.
- Brindley, E.L. (1991). Response of European robins to playback of song : neighbour recognition and overlapping. - *Anim. Behav.* 41, p. 503-512.
- Brooke, M de L. (1978). Sexual differences in the voice and individual vocal recognition in the manx shearwater (*Puffinus puffinus*). - *Anim. Behav.* 26, p. 622-629.

- Brooks, R.J. & Falls, J.B. (1975). Individual recognition by song in white-throated sparrows. III. Song features used in individual recognition. - *Canad. J. Zool.* 53, p. 1749-1761.
- Brown, J.L. (1964). The evolution of diversity in avian territorial systems. - *Wilson Bull.* 76, p. 160-169.
- Brown, J.L. (1982). The adaptationist program. - *Science* 217, p. 884-886.
- Bunnell, P. (1973). Vocalizations in the territorial behaviour of the frog, *Dendrobates pumilio*. - *Copeia* 1973, p. 277-284.
- Carnes, B.A. & Slade, N.A. (1988). The use of regression for detection of competition with multicollinear data. - *Ecology* 69, p. 1266-1274.
- Carpenter, C.C. (1960). Aggressive behaviour and social dominance in the six-lined racerunner (*Cnemidophorus sexlineatus*). - *Anim. Behav.* 8, p. 61-66.
- Carpenter, C.C. (1967). Aggression and social structure in iguanid lizards. - In: *Lizard ecology : a symposium* (W.W. Milstead, ed). University of Missouri Press, Columbia, p. 87-105.
- Carpenter, G.C. (1995). Modeling dominance : the influence of size, coloration, and experience on dominance relations in tree lizards (*Urosaurus ornatus*). - *Herp. Monog.* 9, p. 88-101.
- Catchpole, C. Leisler, B. & Winkler, H. (1985). Polygyny in the great reed warbler, *Acrocephalus arundinaceus* : a possible case of deception. - *Behav. Ecol. Sociobiol.* 16, p. 285-291.
- Censky, E.J. (1995). Mating strategy and reproductive success in the teiid lizard, *Ameiva plei*. - *Behaviour* 132, p. 529-557.
- Chaiken, M. (1992). Individual recognition of nestling distress screams by European starlings (*Sturnus vulgaris*). - *Behaviour* 120, p. 139-150.

- Cheney, D.L. & Seyfarth, R.M. (1980). Vocal recognition in free-ranging vervet monkeys. - *Anim. Behav.* 28, p. 362-367.
- Cheney, D.L., Seyfarth, R.M. & Silk, J.B. (1995). The role of grunts in reconciling opponents and facilitating interactions among adult female baboons. - *Anim. Behav.* 50, p. 249-257.
- Clark, D.C. & Moore, A.J. (1995). Social communication in the Madagascar hissing cockroach : features of male courtship hisses and a comparison of courtship and agonistic hisses. - *Behaviour* 132, p. 401-417.
- Cloudsley-Thompson, J.L. (1972). Site tenure and selection in the African gecko *Tarentola annularis* (Geoffroy). - *Brit. J. Herp* 4, p. 286-292.
- Clutton-Brock, T.H. (1989). Mammalian mating systems. - *Proc. R. Soc. Lond.* 236, p. 339-372.
- Clutton-Brock, T.H. & Albon, S.D. (1979). The roaring of red deer and the evolution of honest advertisement. - *Behaviour* 69, p. 145-170.
- Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. (1982). Red deer : behavior and ecology of two sexes. - University of Chicago Press, Chicago.
- Cochran, W.G. (1977). Sampling techniques. - John Wiley, New-York.
- Colgan, P.W. (1978). Modelling. - In: *Quantitative ethology* (P. W. Colgan, ed). John Wiley, New York, p. 314-329.
- Conner, D.A. (1985a). Analysis of the vocal repertoire of the adult pikas: ecological and evolutionary perspectives. - *Anim. Behav.* 33, p. 124-134.
- Conner, D.A. (1985b). The function of the pika short call in individual recognition. - *Z. Tierpsychol.* 67, p. 131-143.

- Cope, E.D. (1868). Observations on reptiles of the old world. Art. 11. - Proc. Acad. Nat. Sci. 1868, p. 314-123.
- Cox, H. (1966). Linear versus logarithmic averaging. - J. Acous. Soc. Amer. 39, p. 688-690.
- Crews, D. (1975). Effects of different components of male courtship behaviour on environmentally induced ovarian recrudescence and mating preferences in the lizard, *Anolis corolinensis*. - Anim. Behav. 23, p. 349-356.
- Darwin, C. (1871). The descent of man, and selection in relation to sex. - John Murray, London.
- Davies, N.B. (1978). Ecological questions about territorial behaviour. - In : Behavioural ecology, an evolutionary approach. (J.R. Krebs & N.B. Davies, eds). Sinauer, Massachusetts, p. 317-350.
- Davies, N.B. (1991). Mating systems. - In : Behavioural ecology, an evolutionary approach, 3rd edn (J.R. Krebs & N.B. Davies, eds). Blackwell Scientific Publications, Oxford, p. 263-294.
- Davies, N.B. & Halliday, T.R. (1978). Deep croaks and fighting assessment in toads. - Nature 274, p. 683-685.
- Davies, N.B. & Lundberg, A. (1984). Food distribution and a variable mating system in the dunnock (*Prunella modularis*). - J. Anim. Ecol. 53, p. 895-912.
- Davis, M.S. (1987). Acoustically mediated neighbor recognition in the North American bullfrog, *Rana catesbeiana*. - Behav. Ecol. Sociobiol. 21, p. 185-190.
- Dawkins, R. & Krebs, J.R. (1978). Animal signals : information or manipulation. - In: Behavioural ecology : an evolutionary approach. (J.R. Krebs & N.B. Davies, eds). Blackwell Scientific Publications, Oxford, p. 282-309.

- Dawkins, M.S. & Guilford, T. (1991). The corruption of honest signalling. - *Anim. Behav.* 41, p. 865-873.
- Doherty, J.A. & Gerhardt, H.C. (1984). Acoustic communication in hybrid treefrogs : sound production by males and selective phonotaxis by females. - *J. Comp. Physiol. A.* 154, p. 319-330.
- Downhower, J.F. & Brown, L. (1980). Male preferences of female mottled sculpins, *Cottus bairdi*. - *Anim. Behav.* 28, p. 728-734.
- Dyson, M.L. & Passmore, N.I. (1992). Inter-male spacing and aggression in African painted reed frogs, *Hyperolius marmoratus*. - *Ethology* 81, p. 237-247.
- Dyson, M.L., Passmore, N.I., Bishop, P.J. & Henzi, S.P. (1992). Male behaviour and correlates of mating success in a natural population of African painted reed frogs (*Hyperolius marmoratus*). - *Herpetologica* 48, p. 236-246.
- Eaton, M.L. (1988). Multivariate statistics: a vector space approach. - John Wiley, New York.
- Eens, M., Pinxten, R. & Verheyen, R.F. (1991). Male song as a cue for mate choice in the European starling. - *Behaviour* 116, p. 210-238.
- Elfstöm, S.T. (1990). Individual and species-specific song patterns of rock and meadow pipits : physical characteristics and experiments. - *Bioacoustics* 2, p. 277-301.
- Emlen, S.T. (1968). Territoriality in the bullfrog, *Rana catesbeiana*. - *Copeia* 1968, p. 240-243.
- Emlen, S.T. (1971). The role of song in individual recognition in the indigo bunting. - *Z. Tierpsychol.* 28, p. 241-246.
- Emlen, S.T. & Oring, L.W. (1977). Ecology, sexual selection, and the evolution of mating systems. - *Science* 197, p. 215-223.

- Endler, J.A. (1986). Natural selection in the wild. - Princeton University Press, New Jersey.
- Enquist, M. & Leimar, O. (1983). The evolution of fighting behaviour : decision rules and assessment of relative strength. - J. Theor. Biol. 102, p. 387-410.
- Epsmark, Y. (1971). Individual recognition by voice in reindeer mother-young relationship. Field observations and playback experiments. - Behaviour 40, p. 295-301.
- Esser, K. & Schmidt, U. (1989). Mother-infant communication in the lesser spear-nosed bat *Phyllostomus discolor* (Chiroptera, Phyllostomidae) - evidence for acoustic learning. - Ethology 82, p. 156-168.
- Evans, L.T. (1936). The development of the cochlea in the gecko, with special reference to the cochlea-lagena ratio and its bearing on vocality and social behavior. - Anat. Rec. 64, p. 187-201.
- Ewald, P.W. & Rohwer, S. (1982). Effects on supplemental feeding on timing of breeding, clutch size and polygyny in red-winged blackbirds, *Agelaius phoeniceus*. - J. Anim. Ecol. 51, p. 429-450.
- Falls, J.B. (1982). Individual recognition by sound in birds. - In: Acoustic communication in birds, Vol II. Song learning and its consequences (D. E. Kroodsma & E. H. Miller, eds). Academic Press, New York, p. 237-278.
- Falls, J.B. & Brooks, R.J. (1975). Individual recognition by song in white-throated sparrows.II. Effects of location. - Canad. J. Zool. 53, p. 1412-1420.
- Falls, J.B. & McNicholl, M.K. (1979). Neighbor-stranger discrimination by song in male blue grouse. - Can. J. Zool. 57, p. 457-462.
- Falls, J.B. & D'Agincourt, G. (1981). A comparison of neighbour-stranger discrimination in

eastern and western meadowlarks. - Canad. J. Zool. 59, p. 2380-2385.

Faulkes, C.G., Abbott, D.H. & Mellor, A.L. (1990). Investigations of genetic diversity in wild colonies of naked mole-rats (*Heterocephalus glaber*) by DNA fingerprinting. - J. Zool. Lond. 221, p. 87-97.

Fellers, G.M. (1979). Aggression, territoriality and mating behaviour in North American treefrogs. - Anim. Behav. 27, p. 107-119.

Fisher, R.A. (1930). The genetical theory of natural selection. - Clarendon Press, Oxford.

Fitzsimons, V.F.M. (1935). Notes on a collection of reptiles and amphibians made in the Southern kalahari, Bushmanland, and Great and Little Namaqualand. - Ann. Transv. Mus. 15, p. 519-550.

Fleishman, L.J. (1992). The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. - Am. Nat. 139, p. S36-S61.

Forester, D.C., Lykens, D.V. & Harrison, W.K. (1989). The significance of persistent vocalization by the spring peeper, *Pseudacris crucifer* (Anura : Hylidae). - Behaviour 108, p. 197-208.

Francis, R.C. (1983). Experiential effects on agonistic behavior in the paradise fish, *Macropodus opercularis*. - Behaviour 85, p. 292-313.

Frankenberg, E. (1974). Vocalisation of males of three geographical forms of *Ptyodactylus* from Israel (Reptilia: Sauria: Gekkoninae). - J. Herpetol. 8, p. 59-70.

Frankenberg, E. (1978). Calls of male and female tree geckos, *Cyrtodactylus kotschyi*. - Israel J. Zool. 27, p. 53-56.

- Frankenberg, E. (1982). Vocal behavior in the Mediterranean house gecko, *Hemidactylus turcicus*. - *Copeia* 4, p. 770-775.
- Fretwell, S.D. (1972). Populations in a seasonal environment. - Princeton University Press, New Jersey.
- Galleotti, P. & Paven, G. (1991). Individual recognition of male tawny owls (*Strix aluco*) using spectrograms of their territorial calls. - *Ethol. Ecol. Evol.* 3, p. 113-126.
- Gamboa, G.J., Reeve, H.K. & Pfennig, D.W. (1986). The evolution and ontogeny of nestmate recognition in social wasps. - *Ann. Rev. Ecol. Syst.* 31, p. 431-454.
- Garson, P.J. & Hunter, M.L. Jr (1979). Effects of temperature and time of year on the singing behaviour of wrens *Troglodytes troglodytes* and great tits *Parus major*. - *Ibis* 121, p. 481-487.
- Gatz, A.K. (1981). Non-random mating by size in American toads, *Bufo americanus*. - *Anim. Behav.* 29, p. 1004-1012.
- Gelfand, D.L. & McCracken, G.F. (1986). Individual variation in the isolation calls of Mexican free-tailed bat pups (*Tadarida brasiliensis mexicana*). - *Anim. Behav.* 34, p. 1078-1086.
- Gerhardt, H.C. (1975). Sound pressure levels and radiation patterns of the vocalizations of some North American frogs and toads. - *J. Comp. Physiol.* 102, p. 1-12.
- Gerhardt, H.C. (1982). Sound pattern recognition in some North American treefrogs (Anura : Hylidae) : implications for mate choice. - *Amer. Zool.* 22, p. 585-595.
- Gerhardt, H.C. (1988). Acoustic properties used in call recognition by frogs and toads. - In : The evolution of the amphibian auditory systems (B. Fritsch, ed). John Wiley, New York, p. 455-483.

- Gerhardt, H.C. (1994). The evolution of vocalization in frogs and toads. - *Ann. Rev Ecol. Syst.* 25, p. 293-324.
- Gerhardt, H.C. & Mudry, K.M. (1980). Temperature effects on frequency preferences and mating call frequencies in the green treefrog, *Hyla cinerea* (Anura : Hylidae). - *J. Comp. Physiol* 137, p. 1-6.
- Gerhardt, H.C., Daniel, R.E., Perrill, S.A. & Schramm, S. (1987). Mating behaviour and male mating success in the green treefrog. - *Anim. Behav.* 35, p. 1490-1503.
- Gerhardt, H.C., Diekamp, B. & Ptacek, M. (1989). Inter-male spacing in choruses of the spring peeper, *Pseudacris (Hyla) crucifer*. - *Anim. Behav.* 38, p. 1012-1024.
- Gibson, R.M. & Bradbury, J.W. (1985). Sexual selection in lekking sage grouse : phenotypic correlates of male mating success. - *Behav. Ecol. Sociobiol.* 18, p. 117-123.
- Gibson, R.M., Bradbury, J.W. & Vehrencamp, S.L. (1991). Mate choice in lekking sage grouse revisited : the roles of vocal display, female site fidelity and copying. - *Behav. Ecol.* 2, p. 165-180.
- Given, M.C. (1988). Growth rate and the cost of calling activity in male carpenter frogs, *Rana virgatipes*. - *Behav. Ecol. Sociobiol.* 22, p. 153-160.
- Godard, R. (1991). Long-term memory of individual neighbours in a migratory songbird. - *Nature* 350, p. 228-229.
- Godard, R. & Wiley, R.H. (1995). Individual recognition of song repertoires in two wood warblers. - *Behav. Ecol. Sociobiol.* 37, p. 119-123.
- Godwin, G.J. & Roble, S.M. (1983). Mating success in male treefrogs, *Hyla chrysoscelis* (Anura : Hylidae). - *Herpetologica* 39, p. 141-146.

- Goldman, P. (1973). Song recognition by field sparrows. - *Auk* 90, p. 106-113.
- Goldstein, R.B. (1978). Geographic variation in the "hoy" call of the Bobwhite. - *Auk* 95, p. 85-94.
- Goodall, D.W. (1952). Quantitative aspects of plant distribution. - *Biol. Rev.* 27, p. 194-245.
- Gottlander, K. (1987). Variation in the song rate of the male pied flycatcher *Ficedula hypoleuca* : causes and consequences. - *Anim. Behav.* 35, p. 1037-1043.
- Gould, S.J. & Lewontin, R.C. (1981). The spandrels of San Marco and the panglossian paradigm : a critique of the adaptationist programme. - *Proc. Roy. Soc. Lond.* 205, p. 581-598.
- Gould, S.J. & Vrba, E.S. (1982). Exaptation - a missing term in the science of form. - *Paleobiology* 8, p. 4-15.
- Gouzoules, H. & Gouzoules, S. (1990). Matrilineal signatures in the recruitment screams of pigtail macaques, *Macaca nemestrina*. - *Behaviour* 115, p. 327-347.
- Grafen, A. (1987). The logic of diversively asymmetric contests : respect for ownership and the desperado effect. - *Anim. Behav.* 35, p. 462-467.
- Grafen, A. (1990). Biological signals as handicaps. - *J. Theor. Biol.* 144, p. 517-546.
- Grafen, A. (1991). Modelling in behavioural ecology. - In : *Behavioural ecology, an evolutionary approach*, 3rd edn (J.R. Krebs & N.B. Davies, eds). Blackwell Scientific Publications, Oxford, p. 5-31.
- Grahn, M. & Von Schantz, T. (1994). Fashion and age in pheasants : age differences in mate choice. - *Proc. Roy. Soc. Lond.* 253, p. 237-241.
- Gray, J.E. (1865). Descriptions of two new genera of lizards from Damaraland. - *Proc. Zool. Soc.*

Lond. 1865, p. 640-642.

- Greenfield, M.D. (1992). The evening chorus of the desert clicker, *Ligurotettix coquilletti* (Orthoptera : Acrididae) : mating investment with delayed returns. - *Ethology* 91, p. 265-278.
- Greenfield, M.D. (1994). Cooperation and conflict in the evolution of signal interactions. - *Ann. Rev. Ecol. Syst.* 25, p. 97-126.
- Guilford, T. & Dawkins, M.S. (1991). Receiver psychology and the evolution of animal signals. - *Anim. Behav.* 42, p. 1-14.
- Gunther, A. (1865). Reptilia. - *Zool. Rec.* 2, p. 139-162.
- Haacke, W.D. (1964). Description of two new species of lizards and notes on *Fitzimonsia brevipes* (Fitzsimons) from the central namib desert. - *Sci. Pap. Namib. Desert. Res. Stn.* 25, p. 1-14.
- Haacke, W.D. (1969). The call of the barking geckos (Gekkonidae : reptilia). - *Sci. Pap. Namib. Desert. Res. Stn.* 46, p. 83-93.
- Haacke, W.D. (1974). Die bellgeckos des südlichen Africa. - *Natur. u. Mus.* 104, p. 273-279.
- Haacke, W.D. (1975). The burrowing geckos of Southern Africa, 1 (Reptilia, Gekkonidae). - *Annals of the Transvaal Museum* 12, p. 197-243.
- Hafner, G.W., Hamilton, C.L., Steiner, W.W., Thompson, T.J. & Winn, H.E. (1979). Signature information in the song of the humpback whale. - *J. Acoust. Soc. Amer.* 66, p. 1-6.
- Haley, M.P. (1994). Resource-holding power asymmetries, the prior residence effect, and reproductive payoffs in male northern elephant seal fights. - *Behav. Ecol. Sociobiol.* 43, p. 427-434.

- Halliday, T.R. (1983). The study of mate choice. - In : Mate choice (P. Bateson, ed). Cambridge University Press, Cambridge, p. 3-33.
- Halliday, T.R. (1987). Physiological constraints on sexual selection. - In: Sexual selection : testing the alternatives. John Wiley, New York, p. 247-250.
- Halliday, T.R. (1992). Sexual selection in amphibians and reptiles : theoretical issues and new directions. - In : Contributions to herpetology, No. 9. (K. Adler, ed). Society for the Study of Amphibians and Reptiles, Ohio, p. 81-95.
- Halliday, T.R. & Verrell, P.A. (1988). Body size and age in amphibians and reptiles. - J. Herpetol. 22, p. 253-265.
- Halpin, Z.T. (1991). Kin recognition cues of vertebrates. - In: Kin Recognition (P.G Hepper, ed). Cambridge University Press, Cambridge, p. 220-252
- Hamilton, W.D. (1964). The genetical evolution of social behaviour. - J. Theor. Biol. 7, p. 1-52.
- Hamilton, W.D. & Zuk, M. (1982). Heritable true fitness and bright birds : a role for parasites? - Science 218, p. 384-387.
- Hammerschmidt, K. & Todt, D. (1995). Individual differences in vocalisations of young barbary macaques (*Macaca sylvanus*) : a multi-parametric analysis to identify critical cues in acoustic signalling. - Behaviour 132, p. 381-399.
- Hammerstein, P. & Reichert, S.E. (1988). Payoffs and strategies in territorial contests : ESS analyses of two ecotypes of the spider *Agelenopsis aperta*. - Evol. Ecol. 2, p. 115-138.
- Hand, D.J. & Taylor, C.C. (1987). Multivariate analysis of variance and repeated measures. - Chapman & Hall, Cambridge.
- Harper, D.G.C. (1991). Communication. - In : Behavioural ecology, an evolutionary approach,

- 3rd edn (J.R. Krebs & N.B. Davies, eds). Blackwell Scientific Publications, Oxford, p. 374 - 397.
- Harris, M.A. & Lemon, R.E. (1976). Responses of male song sparrows *Melospiza melodia* to neighboring and non-neighbouring individuals. - Ibis 118, p. 421-424.
- Harvey, P.H. & Bradbury, J.W. (1991). Sexual selection. - In : Behavioural ecology, an evolutionary approach, 3rd edn (J.R. Krebs & N.B. Davies, eds). Blackwell Scientific Publications, Oxford, p. 203-233.
- Hempel, C.G. (1966). Philosophy of natural science. - Prentice Hall, New-Jersey.
- Hews, D.K. (1990). Examining hypotheses generated by field experiments of sexual selection on male lizards, *Uta palmeri*. - Evolution 44, p. 1956-1966.
- Hill, G.E. (1991). Plumage coloration is a sexually selected indicator of male quality. - Nature 350, p. 337-339.
- Höglund, J. & Lundberg, A. (1987). Sexual selection in a monomorphic lek-breeding bird : correlates of mate mating success in the great snipe *Gallinago media*. - Behav. Ecol. Sociobiol. 21, p. 211-216.
- Höglund, J. & Robertson, J.G.M. (1988). Chorusing behaviour, a density-dependent alternative mating strategy in male common toads (*Bufo bufo*). - Ethology 79, p. 324-332.
- Horne, R.S. (1995). Spectrogram(2.3) for Windows. Freeware.
- Howard, R.D. (1978). The evolution of mating strategies in bullfrogs *Rana catesbeiana*. - Evolution 32, p. 850-871.
- Hutchinson, J.M., Macnamara, J.M. & Cuthill, I.C. (1993). Song, sexual selection, starvation and strategic handicaps. - Anim. Behav. 45, 1153-1177.

- Hutchinson, R.E., Stevenson, J.G. & Thorpe, W.H. (1968). The basis for individual recognition by voice in the sandwich tern (*Sterna sandvicensis*). - Behaviour 32, p. 150-157.
- Iwasa, U., Pomiankowski, A. & Nee, S. (1991). Quantitative-genetic models for the evolution of costly mate preference. - Evolution 45, p. 1431-1442.
- Jacobs, D.S. & Jarvis, J.U.M. (1996). No evidence for the work-conflict hypothesis in the eusocial naked mole-rat (*Heterocephalus glaber*). - Behav. Ecol. Sociobiol. 39, p. 401-409.
- Jakobsson, S., Radesäter, T. & Järvi, T. (1979). On the fighting behaviour of *Nannacara anomala* males. - Z. Tierpsychol. 49, p. 210-220.
- James, F.C. & McCulloch, C.E. (1990). Multivariate analysis in ecology and systematics : panacea or pandora's box? - Ann. Rev. Ecol. Syst. 21, p. 129-166.
- Jarvis, J.U.M. (1981). Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. - Science 212, p. 571-573.
- Jarvis, J.U.M., O'Riain, M.J. & McDaid, E. (1991). Growth and factors affecting body size in naked mole-rats. - In: The Biology of the Naked Mole-Rat (P.W. Sherman, J.U.M. Jarvis & R.D. Alexander, eds). Princeton University Press, New Jersey, p. 358-383.
- Jennions, M.D. (1993). Female choice in birds and the cost of long tails. - Trends Ecol. Evol. 8, p. 230-232.
- Jennions, M.D., Bishop, P.J., Backwell, P.R.Y. & Passmore, N.I. (1995). Call rate variability and female choice in the African frog, *Hyperolius marmoratus*. - Behaviour 132, p. 709-720.
- Jenssen, T.A. (1970). Female response to filmed displays of *Anolis nebulosus*. - Anim. Behav. 18, p. 640-647.

- Jobson, J. D. (1992). Applied multivariate data analysis. Vol II. - Springer-Verlag, New-York.
- Johnstone, R.A. (1995). Honest advertisement of multiple qualities using multiple signals. - J. Theor. Biol. 177, p. 87-94.
- Johnstone, R.A. & Grafen, A. (1992). The continuous Sir Philip Sidney game : a simple model of biological signalling. - J. Theor. Biol. 156, p. 215-234.
- Jones, G., Hughes, P.M. & Rayner, J.M.V. (1991). The development of vocalizations in *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during post-natal growth and the maintenance of individual vocal signatures. - J. Zool. Lond. 225, p. 71-84.
- Jones, G. & Ransome, R.D. (1993). Echolocation calls of bats are influenced by maternal effects and change over a lifetime. - Proc. R. Soc. Lond. 252, p. 125-128.
- Jones, I. J., Falls, J.B. & Gaston, A.J. (1987). Vocal recognition between parents and young of ancient murrelets, *Synthliboramphus antiquus* (Aves: Alcidae). - Anim. Behav. 35, p. 1405-1415.
- Kacelnic, A. & Krebs, J.R. (1983). The dawn chorus in the great tit (*Parus major*) : proximate and ultimate causes. - Behaviour 83, p. 287-309.
- Kaufmann, J.H. (1983). On the definitions and functions of dominance and territoriality. - Biol. Rev. 58, p. 1-20.
- Kamil, A.C. (1988). Experimental design in ornithology. - Curr. Ornith. 5, p. 313-346.
- Keeley, E.R. & Grant, J.W.A. (1993). Asymmetries in the expected value of food do not predict the outcome of contests between convict cichlids. - Anim. Behav. 45, p. 1035-1037.
- Kendall, M.G. (1962). Rank correlation methods, 3rd edn. - Charles Griffin, London.

- Kirkpatrick, M. (1982). Sexual selection and the evolution of female choice - *Evolution* 36, p. 1-12.
- Kirkpatrick, M. (1985). The evolution of female choice and male parental investment in polygynous species : the demise of the "sexy son". - *Am. Nat.* 125, p. 788-810.
- Kirkpatrick, M. & Ryan, M.J. (1991). The evolution of mating preferences and the paradox of the lek. - *Nature* 350, p. 33-38.
- Kluge, A.G. (1967). Higher taxonomic categories of gekkonid lizards and their evolution. - *Bull. Mus. Nat. Hist.* 135, p. 1-60.
- Klump, G.M. & Gerhardt, H.C. (1987). Use of non-arbitrary acoustic criteria in mate choice by female gray tree frogs. - *Nature* 326, p. 286-288.
- Kodric-Brown, A. & Brown, J.H. (1984). Truth in advertising : the kinds of traits favoured by sexual selection. - *Am. Nat.* 124, p. 309-323.
- Kroodsma, D.E. (1976). The effect of large song repertoires on neighbor "recognition" in male song sparrows. - *Condor* 78, p. 97-99.
- Kroodsma, D.E. (1989). Suggested experimental designs for song playbacks. - *Anim. Behav.* 37, p. 600-609.
- Lacey, E.A. & Sherman, P.W. (1991). Social organization of naked mole-rat colonies: evidence for divisions of labor. - In: *The Biology of the Naked Mole-Rat* (P.W. Sherman, J. U.M. Jarvis & R.D. Alexander, eds). Princeton University Press, New Jersey, p. 275-336.
- Lacey, E.A. & Sherman, P.W. (1996). Cooperative breeding in naked mole-rats: implications for vertebrate and invertebrate sociality. - In: *Cooperative Breeding in Mammals* (N.G. Solomon & J.A. French, eds). Cambridge University Press, Cambridge, p. 267-301.

Lande, R. (1981). Models of speciation by sexual selection on polygenic traits. - *Proc. Natl. Acad. Sci.* 78, p. 3721-3725.

Lande, R. (1987). Genetic correlations between the sexes in the evolution of sexual dimorphism and mating preferences. - In: *Sexual selection : testing the alternatives* (J.W. Bradbury & M. Andersson, eds). John Wiley, Chichester, p. 83-94.

Lande, R. & Arnold, S.J. (1983). The measurement of sexual selection on correlated characters. - *Evolution* 37, p. 1210-1226.

Lanyon, W.E. (1978). A revision of the myiarchus flycatchers of South America. - *Bull. Amer. Mus. Nat. His.* 161, p. 427-628.

Lee, J.C. (1982). Accuracy and precision in anuran morphometrics: Artifacts of preservation. - *Syst. Zool.* 31, p. 266-281.

Leimar, O. & Enquist, M. (1984). The effect of asymmetries in owner-intruder interactions. - *J. Theor. Biol.* 111, p. 475-491.

Lessells, C.M. (1991). The evolution of life histories. - In : *Behavioural ecology, an evolutionary approach*, 3rd edn (J.R. Krebs & N.B. Davies, eds). Blackwell Scientific Publications, Oxford, p. 32-68.

Lessells, C.M. & Boag, P.T. (1987). Unrepeatable repeatabilities : a common mistake. - *Auk* 104, p. 116-121.

Lessells, C.M., Rowe, C.L. & McGregor, P.K. (1995). Individual and sex differences in the provisioning calls of European bee-eaters. - *Anim. Behav.* 49, p. 244-247.

Leuck, B.E. (1995). Territorial defence by male green anoles : an experimental test of the roles of residency and resource quality. - *Herp. Monog.* 9, p. 63-74.

- Licht, L.E. (1976). Sexual selection in toads (*Bufo americanus*). - Can. J. Zool. 54, p. 1277-1284.
- Lieblisch, A.K., Newman, J.D., Shapiro, M. & Symmes, D. (1980). Development of the isolation peep in laboratory-bred squirrel monkeys. - Anim. Behav. 28, p. 1-9.
- Linsenmair, K. E. (1987). Kin recognition in subsocial arthropods, in particular in the desert isopod *Hemilepistus reaumuri*. - In: Kin recognition in animals (D.J.C. Fletcher & C.D. Michener, eds). John Wiley, Chichester, p. 121-208.
- Loesche, P., Stoddard, P.K., Higgins, B.J. & Beecher, M.D. (1991). Signature versus perceptual adaptations for individual vocal recognition in swallows. - Behaviour 118, p. 15-25.
- Loffredo, C.A. & Borgia, G. (1986). Sexual selection, mating systems, and the evolution of avian acoustical displays. - Am. Nat. 128, p. 773-794.
- Loftus-Hills, J.J. & Littlejohn, M.J. (1971). Mating call sound intensities of anuran amphibians. - J. Acoust. Soc. Am. 49, p. 1327-1329.
- Lopez, P.T. & Narins, P.M. (1991). Mate choice in the neotropical frog, *Eleutherodactylus coqui*. - Anim. Behav. 41, p. 757-772.
- Loveridge, A. (1947). Revision of the African Lizards of the family Gekkonidae. - Bull. Mus. Comp. Zool. 98, p. 1-469.
- MacNally, R.C. (1981). On the reproductive energetics of chorusing males : energy depletion profiles, restoration and growth in two sympatric species of *Ranidella* (Anura). - Oecologia 51, p. 118-188.
- MacNally, R.C. (1984). On the reproductive energetics of chorusing males : costs and patterns of call production in two sympatric species of *Ranidella* (Anura). - Oikos 42, p. 82-91.
- Maier, V., Rasa, A.E. & Scheich, H. (1983). Call-system similarity in a ground-living social bird

and a mammal in the bush habitat. - Behav. Ecol. Sociobiol. 12, p. 5-9.

Manley, G.A. (1990). The hearing of geckos. - In : Peripheral hearing mechanisms in reptiles and birds. Springer-Verlag, Berlin, p. 151-164.

Manning, J.T. (1985). Choosy females and correlates of male age. - J. Theor. Biol. 116, p. 348-354.

Marcellini, D.L. (1974). Acoustic behavior of the gekkonid lizard, *Hemidactylus frenatus*. - Herpetologica 30, 44-52.

Marcellini, D.L. (1977). The function of a vocal display of the lizard *Hemidactylus frenatus* (Sauria : Gekkonidae) - Anim. Behav. 25, p. 414-417.

Marler, P. & Hobbet, L. (1975). Individuality in a long-range vocalization of wild chimpanzees. - Z. Tierpsychol. 38, p. 97-109.

Marler, C.A., Walsberg, G., White, M.L. & Moore, M. (1995). Increased energy expenditure due to increased territorial defense in male lizards after phenotypic manipulation. - Behav. Ecol. Sociobiol. 37, p. 225-231.

Marshall, R. & Cherry, M. (1995). An overview of the breeding biology of two sympatric species of barking gecko, *Ptenopus kochi* and *P. garrulus*. Unpublished report submitted to the University of Stellenbosch, South Africa.

Marten, K. & Marler, P. (1977). Sound transmission and its significance for animal vocalization 1. temperate habitats. - Behav. Ecol. Sociobiol. 2, p. 271-290.

Masters, W.M., Raver, K.A.S. & Kazial, K.A. (1995). Sonar signals of big brown bats, *Eptesicus fuscus*, contain information about individual identity, age and family affiliation. - Anim. Behav. 50, p. 1243-1260.

- Maynard Smith, J. (1974). The theory of games and the evolution of animal conflicts. - J. Theor. Biol. 47, p. 209-221.
- Maynard Smith, J. (1987). Sexual selection - a classification of models. - In: Sexual selection : testing the alternatives (J.W. Bradbury & M.B. Andersson, eds). John Wiley, Chichester, p. 9-20.
- Maynard Smith, J. (1991). Theories of sexual selection. - Trends Ecol. Evol. 6, p. 146-151.
- Maynard Smith, J. & Parker, G.A. (1976). The logic of asymmetric contests. - Anim. Behav. 24, p. 159-175.
- Maynard Smith, J. & Harper, D.G.C. (1995). Animal signals : models and terminology. - J. Theor. Biol. 177, p. 305-311.
- Mayr, E. (1972). Sexual selection and natural selection. - In : Sexual selection and the descent of man (B. Campbell, ed). Aldine, Chicago, p. 87-104.
- McArthur, P.D. (1982). Mechanisms of parent-young vocal recognition in the pinon jay (*Gymnorhinus cyanocephalus*). - Anim. Behav. 30, p. 62-74.
- McGregor, P.K. (1991). The singer and the song : on the receiving end of bird song. - Biol. Rev. 66, p. 57-81.
- McGregor, P.K. & Byle, P. (1992). Individually distinctive bittern booms: potential as a census tool. - Bioacoustics 4, p. 93-109.
- McLachlan, G. J. (1992). Discriminant analysis and statistical pattern recognition. - John Wiley, New York.
- Mertens, R. (1946). Die warn- und droh-reaktionen der reptilien. - Abb. senckenb. naturf. Gen. 471, p. 1-108.

- Mertens, R. (1955). Die amphibien und reptilien Südwestafrikas. - Abb. senckenb. naturf. Gen. 490, p. 1-172.
- Michelsen, A. (1978). Sound reception in different environments. - In: Sensory ecology, review and perspectives (M.A. Ali, ed). Plenum Press, New York, p. 345-373.
- Michener, C.D. & Smith, B.H. (1987). Kin recognition in primitively eusocial insects. - In: Kin recognition in animals (D.J.C. Fletcher & C.D. Michener, eds). John Wiley, Chichester, p. 209-242.
- Milinski, M. & Parker, G.A. (1991). Competition for resources. - In : Behavioural ecology, an evolutionary approach, 3rd edn (J.R. Krebs & N.B. Davies, eds). Blackwell Scientific Publications, Oxford, p. 137-168..
- Miller, D.B. (1978). Species-typical and individually distinctive acoustic features of crow calls of red jungle fowl. - Z. Tierpsychol. 47, p. 182-193.
- Moles, A. (1963). Animal language and information theory. - In: Acoustic behaviour of animals (R.G. Busnel, ed.). Elsevier Publishing Company, Amsterdam, p. 112-131.
- Morris, M.R. (1989). Female choice of large males in the treefrog *Hyla chrysoscelis* : the importance of identifying the scale of choice. - Behav. Ecol. Sociobiol. 25, p. 275-281.
- Morris, M.R. & Yoon, S.L. (1989). A mechanism for female mate choice of large males in the treefrog *Hyla chrysoscelis*. - Behav. Ecol. Sociobiol. 25, p. 65-71.
- Møller, A.P. (1994). Sexual selection and the barn swallow. - Oxford University Press, Oxford.
- Morten, E.S. (1975). Ecological sources of selection on avian sounds. - Am. Nat. 108, p. 17-34.
- Morton, M.L. (1981). Seasonal changes in total body lipid and liver weight in the Yosemite toad.

- Copeia 1981, p. 234-238.

Mundinger, P.C. (1970). Vocal imitation and individual recognition of finch calls. - Science 168, p. 480-482.

Myrberg, A.A. (1971). Social dominance and territoriality in the bicolor damselfish,
Eupomacentrus particus (Poey) (Pisces: Pomacentridae). - Behaviour 41, p. 207- 231.

Myrberg, A.A., Kramer, E. & Heinecke, P. (1965). Sound production by three cichlid fishes. -
Science 149, p. 555-558.

Myrberg, A.A. & Riggio, R.J. (1985). Acoustically mediated individual recognition by a coral reef
fish (*Pomacentrus partitus*). - Anim. Behav. 33, p. 411-416.

Nel, J.A.J. & Nolte, H. (1965). Notes on the prey of owls in the Kalahari Gemsbok National
Park, with special reference to small mammals. - Koedoe 8, p. 75-81.

Neter, J., Wasserman, W. & Whitmore, G.A. (1988). Applied statistics, 3rd edn. - Allyn &
Bacon, Massachusetts.

Nevo, E. & Capranica, R.R. (1985). Evolutionary origin of ethological reproductive isolation in
cricket frogs, *Acris*. - In : Evolutionary biology (M.K. Hecht, B. Wallace & G.T. France, eds).
Plenum Press, New York, Vol. 19, p. 147-214.

Niblick, HA., Rostal, D.C. & Classen, T. (1994). Role of male-male interactions and female
choice in the mating system of the desert tortoise, *Gopherus agassizii*. - Herp. Monog. 8. p.
124-132

Nielsen, B.M.B., & Vehrencamp, S.L. (1995). Responses of song sparrows to song-type
matching via interactive playback. - Behav. Ecol. Sociobiol. 37, p. 109-117.

Nur, N. & Hasson, O. (1984). Phenotypic plasticity and the handicap principle. - J. Theor. Biol. 110, p. 275-297.

- Obrist M.K. (1995). Flexible bat echolocation : the influence of individual, habitat and conspecifics on sonar signal design. - Behav. Ecol. Sociobiol. 36, p. 207-219.
- O'Donald, P. (1980). Sexual selection by female choice in a monogamous bird : Darwins theory corroborated. - Heredity 45, p. 201-217.
- Olsson, M. (1992). Contest success in relation to size and residency in male sand lizards, *Lacerta agilis*. - Anim. Behav. 44, p. 386-388.
- O'Riain, M.J. & Jarvis, J.U.M. (1997). Colony member recognition and xenophobia in the naked mole-rat. - Anim. Behav. 53, p. 487-498.
- Otte, D. (1974). Effects and functions in the evolution of signalling systems. - Ann. Rev. Ecol. Syst. 5, p. 385-417.
- Overall, K.L. (1994). Lizard egg environments. - In: Lizard ecology - historical and experimental perspectives (L.J. Vitt & E.R. Pianka, eds). Princeton University Press, New Jersey, p. 51-72.
- Park, T.J. & Dooling, R.J. (1985). Perception of species-specific contact calls by budgerigars (*Melopsittacus undulatus*). - J. Comp. Psychol. 99, p. 391-402.
- Park, T.J., Okanoya, K. & Dooling, R.J. (1985). Operant conditioning of small birds for acoustic discrimination. - J. Ethol. 3, p. 5-9.
- Parker, G.A. (1974). Assessment strategy and the evolution of fighting behaviour. - J. Theor. Biol. 47, p. 223-243.
- Parker, G.A. (1978). Searching for mates. - In: Behavioural ecology : an evolutionary approach (J.R. Krebs & N.B. Davies), Blackwell Scientific Publications, Oxford, p. 214-244.
- Parker, G.A. (1983). Mate quality and mating decisions. - In: Mate choice (P. Bateson, ed). Cambridge University Press, Cambridge, p. 141-166.

- Partridge, L. & Halliday, T. (1984). Mating patterns and mate choice. - In : Behavioural ecology : an evolutionary approach, 2nd edn (J.R. Krebs & N.B. Davies, eds). Blackwell Scientific Publications, Oxford, p. 222-250.
- Passmore, N.I. (1981). Sound levels of mating calls of some African frogs. - *Herpetologica* 37, p. 166-171.
- Passmore, N.I., Bishop, P.J. & Caithness, N. (1992). Calling behaviour influences mating success in male painted reed frogs, *Hyperolius marmoratus*. - *Ethology* 92, p. 227-241.
- Pepper, J.W., Braude, S.H., Lacey, E.A. & Sherman, P.W. (1991). Vocalizations of the naked mole-rat. - In: The Biology of the Naked Mole-Rat (P.W. Sherman, J.U.M. Jarvis & R.D. Alexander, eds). Princeton University Press, New Jersey, p. 243-274.
- Pereira, M.E. (1986). Maternal recognition of juvenile offspring coo vocalizations in Japanese macaques. - *Anim. Behav.* 34, p. 935-937.
- Petronovich, L. (1974). Individual recognition of pup vocalization by northern elephant seal mothers. - *Z. Tierpsychol.* 34, p. 308-312.
- Pianka, E.R. & Parker, W.S. (1975). Age-specific reproductive tactics. - *Am. Nat.* 109, p. 453-464.
- Pickstock, J.C. & Krebs, J.R. (1980). Neighbour-stranger discrimination in the chaffinch (*Fringilla coelebs*). - *J. Ornith.* 121, p. 105-108.
- Pielou, E.C. (1962). The use of plant-to-neighbour distances for the detection of competition. - *J. Ecol.* 50, p. 357-367.
- Pielou, E.C. (1977). Mathematical ecology. - John Wiley, New York.
- Pierce, J. R. (1961). Symbols, signals and noise - the nature and process of communication. -

Harper and Row, London.

Pimentel, R.A. & Frey, D.F. (1978). Multivariate analysis of variance and discriminant analysis. - In: Quantitative ethology (P. W. Colgan, ed). John Wiley, New York, p. 247-274

Poindron, P. & Carrick, M.J. (1976). Hearing recognition of the lamb by its mother. - Anim. Behav. 24, p. 600-602.

Polakow, D.A., Backwell, P.R.Y, Caithness, N. & Jennions, M.D. (1995). Stabilizing or directional selection in signalling systems : Investigations in a population of painted reed frogs, *Hyperolius marmoratus*. - S. Afr. J. Sci 91, p. 270-273.

Pomiankowski, A.N. (1987). The 'handicap principle' does work - sometimes. - Proc. Roy. Soc. Lond. B127, p. 123-145.

Pomiankowski, A.N. (1988). The evolution of female mate preferences for male genetic quality. - Oxford Surv. Evol. Biol. 5, p. 136-184.

Ramer, J.D., Jenssen, T.A. & Hurst, C.J. (1983). Size-related variation in the advertisement call of *Rana clamitans* (Anura : Ranidae), and its effect on conspecific males. - Copeia 1983, p. 141-155.

Rand, A.S. (1967). The adaptive significance of territoriality in iguanid lizards. - In: Lizard ecology : a symposium (W.W. Milstead, ed). University of Missouri Press, Columbia, p. 106-116.

Rao, C.R. (1966). Covariance adjustment and related problems in multivariate analysis. - In: Multivariate Analysis (P. R. Krishnaiah, ed). Academic Press, New York, p. 87-103.

Reeve, H.K. (1992). Queen activation of lazy workers in colonies of the eusocial naked mole-rat. - Nature 358, p. 147-149.

- Reeve, H.K., Westneat, D.F., Noon, A., Sherman, P.W. & Aquadro, C.F. (1990). DNA 'fingerprinting' reveals high levels of inbreeding in the eusocial naked mole-rat. - *Proc. Natl. Acad. Sci.* 87, p. 2496-2500.
- Reeve, H.K. & Sherman, P.W. (1993). Intracolony aggression and nepotism by the breeding female naked mole-rat. - In: *The Biology of the Naked Mole-Rat* (P.W. Sherman, J.U.M. Jarvis & R.D. Alexander, eds). Princeton University Press, New Jersey, p. 337-357.
- Reeve, H.K. & Sherman, P.W. (1991). Adaptation and the goals of evolutionary research. - *Q. Rev. Biol.* 68, p. 1-32.
- Reid, M.L. (1987). Costliness and reliability in the singing vigour of Ipswich sparrows. - *Anim. Behav.* 35, p. 1735-1743.
- Reid, M. L. and Weatherhead, P. J. (1990) Mate-choice criteria of Ipswich sparrows: the importance of variability. - *Anim. Behav.* 40, p. 538-544.
- Rice, W.R. (1989). Analyzing tables of statistical tests. - *Evolution* 43, 223-225.
- Richards, D.G. (1979). Recognition of neighbors by associative learning in rufous-sided towhees. - *Auk* 96, p. 688-693.
- Riechert, S.E. (1979). Games spiders play : II. Resource assessment strategies. - *Behav. Ecol. Sociobiol.* 6, p. 121-128.
- Rietke, M.E. & Semlitsch, R.D. (1991). Mating behavior and determinants of male mating success in the gray treefrog, *Hyla chrysoscelis*. - *Can. J. Zool.* 69, p. 246-250.
- Ritchie, M.G., Couzin, I.D. & Snedden, W.A. (1995). What's in a song? Female bushcrickets discriminate against the song of older males. - *Proc. R. Soc. Lond.* 262, p. 21-27.
- Robertson, J.G.M. (1984). Acoustic spacing by breeding males of *Uperoleia regosa* (Anura:

Leptodactylidae). - Z. Tierpsychol. 64, p. 283-297.

Robertson, J.G.M. (1986). Male territoriality, fighting and assessment of fighting ability in the Australian frog, *Uperoleia regosa*. - Anim. Behav. 34, p. 763-772.

Robinson, M.D. & Haacke, W.D. (1977). The call of the south African baking gecko, *Ptenopus* : comments on its evolution and function. - Am. Soc. Ichthyologists and Herpetologists 57th Ann. Meeting. University of Florida, Gainesville.

Robisson, P., Aubin, T. & Bremond, J. (1993). Individuality in the emperor penguin *Aptenodytes forsteri*: adaptation to a noisy environment. - Ethology 94, p. 279-290.

Rohlf, F.J. & Archie, J.W. (1978). Least-squares mapping using interpoint distances. - Ecology 59, p. 126-132.

Rosenberg, R.H. & Enquist, M. (1991). Contest behaviour in Weidemeyer's admiral butterfly *Limenitis weidemeyerii* (Nymphalidae) : the effect of size and residency. - Anim. Behav. 42, p. 805-811.

Ruby, D.E. (1984). Male breeding success and differential access to females in *Anolis carolinensis*. - Herpetologica 40, p. 272-280.

Ryan, M.J. (1980). Female mate-choice in the neotropical frog. - Science 209, p. 523-525.

Ryan, M.J. (1983). Sexual selection and communication in the neotropical frog, *Physalaemus pustulosus*. - Evolution 37, p. 261-272.

Ryan, M.J. (1985). The Tungara Frog : A study in sexual selection and communication. - University of Chicago Press, Chicago

Ryan, M.J. (1988). Energy, calling, and selection. - Amer. Zool. 28, p. 885-898.

- Ryan, M.J. & Keddy-Hector, A. (1992). Directional patterns of female mate choice and the role of sensory biases. - *Am. Nat.* 139, p. S4-S35.
- Sakaluk, S.K. & Belwood, J.J. (1984). Gecko phonotaxis to cricket calling song : a case of satellite predation. - *Anim. Behav.* 32, p. 659-662.
- Sayigh, L.S., Tyack, P.L., Wells, R.S., Scott, M.D. & Irvine, A.B. (1995). Sex differences in signature whistle production of free-ranging bottlenose dolphins, *Tursiops truncatus*. - *Behav. Ecol. Sociobiol.* 36, p. 171-177.
- Scherrer, J.A. & Wilkinson, G.S. (1993). Evening bat isolation calls provide evidence for heritable signatures. - *Anim. Behav.* 46, p. 847-860.
- Schieffelin, J.S. & Sherman, P.W. (1995). Tugging contests reveal feeding hierarchies in naked mole-rat colonies. - *Anim. Behav.* 49, p. 537-541.
- Schoener, T.W. (1977). Competition and the niche. - In: *Biology of the reptilia*, Vol. 7 (C. Gans, ed). Academic Press, London, p. 35-136.
- Schubert, M. (1976). Über die variabilität von lockrufen des gimpels *Pyrrhula pyrrhula*. - *Ardea* 64, p. 62-71.
- Schwartz, J.J. (1986) Male calling behavior and female choice in the neotropical treefrog, *Hyla microcephala*. - *Ethology* 73, p. 116-127.
- Schwartz, J.J. (1987). The function of call alternation in anuran amphibians : a test of three hypotheses. - *Evolution* 41, p. 461-471.
- Schwartz, J.J. & Rand, A.S. (1991). The consequences for communication of call overlap in the tungara frog, a Neotropical anuran with a frequency-modulated call. - *Ethology* 89, p. 73-83.
- Scott, D.W. (1992). Multivariate density estimation. - John Wiley, New York.

- Seale, D.B. (1987). Amphibia. - In: Animal energetics (F.J. Vernberg & T.J. Pandian, eds). Academic Press, New York, Vol. 1, p. 467-551.
- Searcy, W.A. (1979). Sexual selection and body size of male red-winged blackbirds. - *Evolution* 33, p. 649-661.
- Searcy, W.A., McArthur, P.D., Peters, S.S. & Marler, P. (1982). Response of male song and swamp sparrows to neighbour, stranger, and self songs. - *Behaviour* 77, p. 152-163.
- Seeley, T.D. (1985). Honeybee Ecology. - Princeton University Press, New Jersey.
- Seyfarth, R.M., Cheney, D.L. & Marler, P. (1980). Vervet monkey alarm calls: semantic communication in a free-ranging primate. - *Anim. Behav.* 28, p. 1070-1094.
- Shannon, C.E. & Weaver, W. (1949). The mathematical theory of communication. - University of Illinois Press, Urbana.
- Shine, R. (1978). Sexual size dimorphism and male combat in snakes. - *Oecologia* 33, p. 269-277.
- Sieber, O. J. (1985). Individual recognition of parental calls by bank swallow chicks (*Riparia riparia*). - *Anim. Behav.* 33, p. 107-116.
- Sieber, O.J. (1986). Acoustic recognition between mother and cubs in racoons (*Procyon lotor*). - *Behaviour* 96, p. 130-163.
- Siegel, S. & Castellan, N.J. Jr. (1988). Nonparametric statistics for the behavioural sciences. - MacGraw-Hill, New York.
- Sigmund, W.R. (1983). Female preference for *Anolis carolinensis* males as a function of dewlap color and background coloration. - *J. Herpetol.* 17, p. 137-143.

- Sigursj ndottir, H. & Parker, G.A. (1981). Dung-fly struggles : evidence for assessment strategy.
- Behav. Ecol. Sociobiol. 8, p. 219-230.
- Simmons, L.W. & Zuk, M. (1992). Variability in call structure and pairing success of male field crickets, *Gryllus bimaculatus* : the effects of age, size and parasite load. - Anim. Behav. 44, p. 1145-1152.
- Simmons, R. E. (1988) Food and the deceptive acquisition of mates by polygynous male harriers.
- Behav. Ecol. Sociobiol. 23, p 83-92.
- Snowdon, C.T. & Cleveland, J. (1980). Individual recognition of contact calls by pygmy marmosets. - Anim. Behav. 28, p. 717-727.
- Sokal, R.R & Rohlf, F.J. (1981). Biometry, 2nd edn. - W.H. Freeman, San Francisco.
- Soundblaster. (1994). Soundblaster AWE32. - Creative Technology Ltd, Singapore
- Stamps, J.A. (1977). Social behavior and spacing patterns in lizards. - In: Biology of the reptilia, Vol. 7 (C. Gans, ed). Academic Press, London, p. 265-334.
- Stamps, J.A. (1983a). Sexual selection, sexual dimorphism, and territoriality. - In: Lizard Ecology (R.B. Huey, E.R. Pianka & T.W. Schoener, eds). Harvard University Press, Cambridge, p. 169-204.
- Stamps, J. (1983b). Territoriality and the defense of predator-refuges in juvenile lizards. - Anim. Behav. 31, p. 857-870.
- STATGRAPHICS. (1992). STATGRAPHICS version 6. - Statistical Graphics Corporation, Massachusetts.
- STATISTICA. (1995). STATISTICA for Windows. - Statsoft Inc, Oklahoma.

- Steiner, W.W. (1981). Species-specific differences in pure tonal whistle vocalizations of five western north Atlantic dolphin species. - Behav. Ecol. Sociobiol. 9, p. 241-246.
- Stevenson, J.G., Hutchinson, R.E., Hutchinson, J.B., Bertram, B.C.R. & Thorpe, W.H. (1970). Individual recognition by auditory cues in the common tern (*Sterna hirundo*). - Nature 226, p. 562-563.
- Stoddard, P.K., Beecher, M.D., Horing, C.L. & Campbell, S.E. (1991). Recognition of individual neighbors by song in the song sparrow, a species with song repertoires. - Behav. Ecol. Sociobiol. 29, p. 211-215.
- Stoddard, P.K., Beecher, M.D., Loesche, P. & Campbell, S.E. (1992). Memory does not constrain individual recognition in a bird with song repertoires. - Behaviour 122, p. 274-287.
- Sullivan, B.K. (1982). Significance of size, temperature and call attributes to sexual selection in *Bufo woodhousei australis*. - J. Herpetol. 16, p. 103-106.
- Sullivan, B.K. (1983). Sexual selection in the Great Plains toad (*Bufo cognatus*). - Behaviour 84, p. 258-264.
- Sullivan, B.K. & Walsberg, G.E. (1985). Call rate and aerobic capacity in Woodhouse's toad (*Bufo woodhousei*). - Herpetologica 41, p. 404-407.
- Sutherland, W.J. & De Jong, M.C.M. (1991). The evolutionary stable strategy for secondary sexual characters. - Behav. Ecol. 2, p. 16-20.
- Symmes, D., Newman, J.D., Talmage-Riggs, G. & Lieblich, A.K. (1979). Individuality and stability of isolation peeps in squirrel monkeys. - Anim. Behav. 27, p. 1142-1152.
- SYSTAT. (1992). SYSTAT for Windows, Version 5 - SYSTAT, Evanston, Illinois.
- Taigen, T.L. & Wells, K.D. (1985). Energetics of vocalization by an anuran amphibian (*Hyla*

versicolor). - J. Comp. Physiol 155, p. 163-170.

Telford, S.R. (1985). Mechanisms and evolution of inter-male spacing in the painted reedfrog (*Hyperolius marmoratus*). - Anim. Behav. 33, p. 1353-1361.

Thiele, D. & Bailey, W.J. (1980). The function of sound in male spacing behaviour in bush crickets (Tettigoniidae, Orthoptera). - Aust. J. Zool. 5, p. 275-286.

Thomson, S. (1986) Male spawning success and female mate choice in the mottled sculpin, *Forsterygion varium* (Pisces: Tripterygiidae). - Anim. Behav. 34. p. 580-589.

Thornhill, R. (1981). *Panorpa* (Mecoptera : Panorpidae) scorpionflies : systems for understanding resource-defence polygyny and alternative male reproductive efforts. - Ann. Rev. Ecol. Syst. 12, p. 355-386.

Thornhill, R. & Alcock, J. (1983). The evolution of insect mating systems. - Harvard University Press, Massachusetts.

Thornhill, R. & Sauer, P. (1992). Genetic sire effects on the fighting ability of sons and daughters and mating success of sons in a scorpionfly. - Anim. Behav. 43, p. 255-264.

Toaka, M., Sato, T., Kamada, T. & Okumura, H. (1989). Sexual dimorphism of chatter-calls and vocal sex recognition in leach's storm-petrels (*Oceanodroma leucorhoa*). - Auk 106, p. 498-501.

Tokarz, R.R. (1985). Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). - Anim. Behav. 33, p. 746-753.

Tokarz, R.R. (1995). Mate choice in lizards : a review. - Herp. Monog. 9, p. 17-40.

Tooze, Z.J., Harrington, F.H. & Fentress, J.C. (1990). Individual distinct vocalizations in timber wolves, *Canis lupus*. - Anim. Behav. 40, p. 723-730.

- Trivers, R.I. (1972). Parental investment and sexual selection. - In: Sexual selection and the descent of man (B. Campbell, ed). Aldine Publishing Co., Chicago, p. 136-179.
- Trivers, R.I. (1974). Sexual selection and resource-accruing abilities in *Anolis garmani*. - Evolution 30, p. 253-269.
- Turner, G.F. (1994). The fighting tactics of male mouthbrooding cichlids : the effects of size and residency. - Anim. Behav. 47, p. 655-662.
- Turner, G.F. & Huntingford, F.A. (1986). A problem for game theory analysis : assessment and intention in male mouthbrooder contests. - Anim. Behav. 34, p. 961-970.
- Underwood, G. (1954). On the classification and evolution of geckos. - Proc. Zool. Soc. Lond. 124, p. 469-492.
- Veen, J. (1986). The crested tern and the supermarket. - Anim. Behav. 34, p. 937-939.
- Vehrencamp, S.L., Bradbury, J.W. & Gibson, R.M. (1989). The energetic cost of display in male sage grouse. - Anim. Behav. 38, p. 885-896.
- Von Schantz, T., Goransson, G., Andersson, G., Froberg, I., Grahn, M. Helgee, A. & Wittzell, H. (1989). Female choice selects for viability-based male trait in pheasants. - Nature 337, p. 166-169.
- Wagner Jr., W.E. (1989). Fighting, assessment, and frequency alteration in Blanchard's cricket frog. - Behav. Ecol. Sociobiol. 25, p. 429-436.
- Warner, R.R. (1984). Deferred reproduction as a response to sexual selection in a coral reef fish : a test of the life historical consequences. - Evolution 38, p. 148-162.
- Warner, R.R. (1990). Male versus female influences on mating site determination in a coral reef

- fish. - Anim. Behav. 39, p. 540-548.
- Waser, P.W. (1977). Individual recognition, intragroup cohesion and intergroup spacing: evidence from sound playback to forest monkeys. - Behaviour 60, p. 28-74.
- Weary, D.M. (1990). Categorization of song notes in great tits : which acoustic features are used and why? - Anim. Behav 39, p. 450-457.
- Weary, D.M., Norris, K.J. & Falls, J.B. (1990). Song features birds use to identify individuals. - Auk 107, p. 623-625.
- Weary, D.M. & Krebs, J.R. (1992). Great tits classify songs by individual voice characteristics. - Anim. Behav. 43, p. 283-287.
- Weeden, J.S. & Falls, J.B. (1959). Differential responses of male ovenbirds to recorded songs of neighbouring and more distant individuals. - Auk 76, p. 343-351.
- Wells, K.D. (1977). Territoriality and male mating success in the green frog (*Rana clamitans*). - Ecology 58, p. 750-762.
- Wells, K.D. (1978). Territoriality in the green frog (*Rana clamitans*) : vocalizations and agonistic behavior. - Anim. Behav. 26, p. 1051-1063.
- Wells, K.D. & Taigen, T.L. (1986). The effects of social interactions on calling energetics in the gray treefrog (*Hyla versicolor*). - Behav. Ecol. Sociobiol. 19, p. 9-18.
- Wells, K.D. & Taigen, T.L. (1989). Calling energetics of a neotropical treefrog, *Hyla microcephala*. - Behav. Ecol. Sociobiol. 25, p. 13-22.
- Werner, Y.L. (1976). Optimal temperatures for inner-ear performance in gekkonid lizards. - J. Exp. Zool. 195, p. 319-352.

- Werner, Y.L., Frankenberg, E. & Adar, O. (1978). Further observation on the distinctive repertoire of *Ptyodactylus hasselquistii* cf. *hasselquistii* (Reptilia : Gekkonidae). - Isr. J. Zool. 27, p. 176-188.
- Wever, E.G., Crowley, D.E. & Peterson, E.A. (1963). Auditory sensitivity in four species of lizards. - J. Aud. Res. 3, p. 151-157.
- Wever, E.G. (1978). The reptile ear. - Princeton, New Jersey.
- White, R.E.C. & White, S.J. (1970). Individual voice production in gannets. - Behaviour 37, p. 40-54.
- White, R.E.C., White, S.J. & Thorpe, W.H. (1970). Acoustic basis for individual recognition by voice in the gannet. - Nature 225, p. 1156-1158.
- Whitney, C.L. & Krebs, J.R. (1975). Spacing and calling in Pacific tree frogs, *Hyla regilla*. - Can. J. Zool. 53, p. 1519-1527.
- Wilczynski, W. & Brenowitz, E.A. (1988). Acoustic cues mediate inter-male spacing in a neotropical frog. - Anim. Behav. 36, p. 1054-1063.
- Wiley, R.H. (1974). Evolution of social organisation and life-history patterns among grouse. - Q. Rev. Biol 49, p. 201-227.
- Wiley, R.H. (1991). Lekking in birds and mammals : behavioral and evolutionary issues. - Adv. Study Behav, 20, p. 210-291.
- Williams, G.C. (1966). Adaptation and natural selection. - Princeton University Press, New Jersey.
- Willmer, P. (1991). Thermal biology and mate acquisition in ectotherms. - Trends Ecol. Evol. 6, p. 396-399.

- Wilson, E.O. (1975). Sociobiology - the new synthesis. - Harvard Univeristy Press, Massachusetts.
- Woolbright, L.L. (1985). Patterns of nocturnal movement and calling by the tropical frog *Eleutherodactylus coqui*. - Herpetologica 41, p. 1-9.
- Woolbright, L.L. & Stewart, M.M.(1987). Foraging success of the tropical frog, *Eleutherodactylus coqui* : the cost of calling. - Copeia 1987, p. 69-75.
- Wunderle, J.M. Jr. (1978). Differential Response of territorial yellowthroats to the songs of neighbours and non-neighbours. - Auk 95, p. 389-395.
- Young, A.M. (1981). Temporal selection for communicatory optimization : the dawn-dusk chorus as an adaptation in tropical cicadas. - Am. Nat 117, p. 826-829.
- Zahavi, A. (1975). Mate selection a selection for a handicap. - J. Theor. Biol. 53, p. 205-214.
- Zahavi, A. (1977). The cost of honesty (further remarks on the handicap principle). - J. Theor. Biol. 67, p. 603-605.
- Zahavi, A. (1993). The fallacy of conventional signalling. - Phil. Trans. R. Soc. Lond B340, p. 227-230.
- Zar, J.H. (1984). Biostatistical analysis, 2nd edn. - Prentice-Hall, New Jersey.

Appendix I

Summary statistics for raw data on morphology, SPL and call descriptors. Mean, standard deviation (s.d.), range and sample size (n) are indicated. Phenotypic data are described for both the 1994 and 1995 field seasons.

<u>Phenotypic</u>	Mean	s.d.	Range	n	Notes?
Mass - male (1994)	5.9 g	1.50	3.8 - 6.6	19	
- male (1995)	6.2 g	0.95	4 - 7.7	23	
Mass - female (1994)	5.8 g	1.03	2 - 6.9	20	
- female (1995)	5.9 g	0.75	3.7 - 6.5	5	
Length - male (1994)	102.3 mm	11.2	84 - 122	19	
- male (1995)	108.6 mm	23.9	87 - 113	23	
Length - female (1994)	99.2 mm	9.27	83 - 112	20	
- female (1995)	111.7 mm	18.3	90 - 140	5	
Yellow - (1994)	13.7 mm	2.14	9 - 18	19	
- (1995)	15.4 mm	1.93	12 - 21	23	
SPL - (1995) (@ 1 m)	71.3 dB	+ 1.2 - 1.7	67.8 - 74	18	dB scale is logarithmic , s.d.'s are therefore asymmetrical about the mean

Call descriptors

AFREQ	2383 Hz	278	1446 - 2918	300
DUR	1407 ms	263	698 - 2194	300
CLICKS	12	1.55	6 - 18	300
RANGE	807 Hz	195	12 - 1270	300
BCI	61.44 s	49.72	10 - 328	300